EDGES, FRUITS, FRUGIVORES, AND SEED DISPERSAL IN A NEOTROPICAL MONTANE FOREST

By

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EDGES, FRUITS, FRUGIVORES, AND SEED DISPERSAL IN A NEOTROPICAL MONTANE FOREST

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Edges resulting from natural or human disturbances influence the distribution of organisms as well as ecological processes. One such process is seed dispersal, which in turn may influence may the location of edges through time and even the entire structure of landscapes. In the Reserva Natural La Planada, Colombia, I investigated how edges resulting from human activities influenced seed dispersal. In particular, I examined how distance from forest edge, in combination with edge age and treefall gaps, could affect recruitment rates, fruit abundance, seed movement, and the distribution of birds in the understory of this neotropical montane forest. Sampling took place at three old (>40 yr) and three new (<15 yr) edges and within each edge at four distances (0-10, 30-40, 60-70, 190-200 m) from the pasture-forest edge.

Edges influenced *Palicoura gibbosa* and *Faramea affinis*, the two most common understory plants, at various stages of their life cycle. Seed predation and seed germination but not relative growth or leaf production rates changed across the pasture-forest edge. The latter, however, were influenced by treefall gaps. At the community level, fruit abundance and the distribution of understory birds changed across the pasture-forest edge in complex ways that not always reflected changes due to the presence of edges. This was demonstrated by the fact that (1) two-way interactions between distance, edge age, treefall gaps, and month were significant, and (2) response variables describing fruit and bird abundance at the community level did not show the same trends.

Edges influenced fruit-frugivore interactions at the level of forest stands but also at the level of entire landscapes as demonstrated by an analysis of body mass distribution of frugivorous birds as a function of ecosystem fragmentation. With more edges, entire groups of birds with similar body mass (termed "lumps") disappeared. Nevertheless, the distribution of body mass, i.e., lump structure, remained almost intact under certain land use types. This work suggests that at broad scales edges influence frugivorous birds and, as a result, seed dispersal.

CHAPTER 1
THE ROLE OF EDGES IN NEOTROPICAL MONTANE LANDSCAPES

Edges constitute a common feature of neotropical montane landscapes. Complex topography and climate in conjunction with natural disturbances, ranging from treefall gaps (Murray 1988; Lawton and Putz 1988; Samper 1992), and landslides (Garwood et al. 1979; Lawton and Dryer 1980; Gentry 1992*b*), to mudflows, have given rise to a heterogeneous landscape in which edges bound the disturbed areas. Over evolutionary time, the dynamic and heterogeneous character of these landscapes may have resulted in the unusually high levels of biodiversity that characterize neotropical montane ecosystems (Terborgh and Winter 1983, Terborgh 1985, Gentry 1986, 1992*a*).

Superimposed on this natural heterogeneity is that resulting from human activities. In areas where favorable conditions prevail patches of forest are immersed in an agricultural and urban matrix. Conversely, in areas where unfavorable conditions limit the development of economic activities, fields, second growth, and urban areas are immersed in a forest matrix. In both situations the areas modified by human activities are bounded by edges. Over shorter time scales than those defined by large-scale natural disturbances, changes in land use have led to extinctions and invasions by an unknown number of species (Henderson et al. 1991, Kattan 1992) .

Even though edges are a prominent feature of neotropical mountains, little is known about how they influence landscape pattern. My dissertation focuses on edges and how they influence seed dispersal through fruit-frugivore interactions. Changes in the nature of fruit-frugivore interactions can provide information on the persistence of edges through time, depending on the ability of plants to produce and disperse their seeds. On the other hand, changes in the composition and number of individuals across edges can provide information on edge structure and productivity.

A common thread among studies focusing on edges is the lack of a common pattern, without which it is difficult to propose underlying causes or even consequences. Each new study has added details at the cost of finding generalities from which testable predictions can be made. In my dissertation I followed two different approaches to the study of edges. Both had as a central theme that of fruit-frugivore interactions. The first generated detailed information on fruit-frugivore interactions at the level of forest stands. Nevertheless, this information precludes generalizations about the role of edges in neotropical montane forests due to the intrinsic characteristics of my study site. The second generated consistent patterns at the level of entire landscapes that differed in degree of transformation by human activities. This portion of the study, therefore, might be useful in generating testable hypotheses that could guide future studies.

My study area and general sampling procedure are described in detail in chapter 2. I often refer to this chapter because the studies I describe in chapters 3 to 5 were based on the same sampling procedure.

In chapter 3 I focus on two understory plants, Palicoura gibbosa and Faramea affinis (Rubiaceae) and ask how edges may influence different components of the life cycle of these two species and how this may influence recruitment. These two species are the most common understory species of my study site and are bird-dispersed. In particular, I looked at how the combined effect of distance from forest edge and presence of treefall gaps affect pollination, fruit set, seed predation, seed germination, and seedling growth.

In chapter 4 I take a broader approach to the study of edges and their influence on fruit-frugivore interactions, by focusing on the assemblage of understory plants. I ask whether fruit abundance changes across pasture-forest edges and how treefall gaps and season modify such effects. I look at changes in fruit abundance for the entire assemblage of understory plants and for individual species. Changes in fruit abundance can affect the distribution of birds feeding on them and thus seed dispersal across edges.

In chapter 5 I keep the previous approach to the study of edges and their influence on fruit-frugivore interactions but ask how edges influence the distribution of understory birds, particularly frugivores. I compare the distribution of nectarivorous, insectivorous, and frugivorous birds across the pasture-forest edge to elucidate possible mechanisms underlying observed patterns.

I take a completely different approach in chapter 6 to the study of edges and their influence on fruit-frugivore interactions. Instead of asking how the distribution of frugivorous birds is affected by the creation of edges within forest stands, I ask how the distribution of frugivorous birds is affected by edges within whole landscapes. I compare changes in the distribution of frugivorous birds across sites that have been modified in various ways by human activities. This approach provides the basis for some generalizations and the formulation of testable hypotheses for future work.

Chapter 7 is the place for synthesis and speculation. I emphasize that edges are part of landscapes that are in continuous change and thus have to be seen as dynamic, not fixed entities of landscapes. Seed dispersers and seeds move between forest interior and edge, and sparse species of plants and frugivorous birds are found more often at edges than at forest interior. These results suggest a critical role of edges in landscapes subject to change.

CHAPTER 2
DESCRIPTION OF STUDY AREA

Study Area

I conducted this study at Reserva Natural La Planada and Finca El Bosque, located in the municipality of Ricaurte, department of Nariño, SW Colombia (78°00'W and 1°10'N) (Fig. 2-1). Both localities lie on the western slope of the Andes at 1,800 m. The biota of La Planada and its surroundings is one of the most diverse of the northern Andes (Terborgh and Winter 1983; Orejuela 1987) and twenty percent of the plant and animal species reported for the area are endemic (geographical range <50,000 km^2, Terborgh and Winter 1983).

Observations were concentrated in the NW and W portions of La Planada and El Bosque, respectively. These two areas lie on the watershed division of the Miraflores and Pialapi rivers. Colonization of this area started in the early 1940s and proceeded from the bottom of the valleys (1,200 m) to the top of the mountains (1,800 m), which are still mostly covered by forest. Small sugarcane plantations, transient corn fields, pastures, fallows, and second-growth vegetation are embedded in the forest matrix. These disturbed areas are concentrated at the bottom of the valleys and range from 1-9

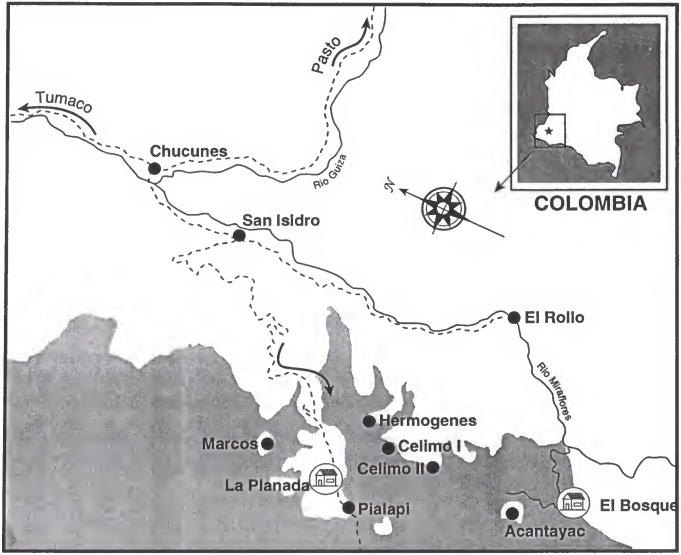


Figure 2-1. Location of study area and edges that were sampled. Forest is represented by shaded area (based on a 1981 aerial photograph, approximate scale 1:26,000)

ha (mode 3 ha) (Gómez and Palau 1994). The patches of forest are connected by strips of forest that have been left along streams, steep sloptes, and mountain ridges.

The natural disturbance regime is varied. At small scales, treefall gaps, which occur mostly during the rainy season, are common (Samper 1992). At larger scales landslides, ash rain (e.g., January 1993 volcanic eruption), and strong winds, the latter resulting in the defoliation of large areas (e.g., August 1993), affect whole landscapes.

Unpublished climatological records of La Planada (1985-1994) show a mean annual rainfall and temperature of 4,437 mm and 19.2°C, respectively (Fig. 2-2). Rainfall is distributed in two wet seasons, interrupted by a mild dry (February-March) and a strong dry (June-August) season (Fig. 2-2). Based on these data, La Planada can be classified as a transitional life zone between tropical premontane rain and wet forest (Holdridge 1967). An important climatological feature of La Planada and its surroundings is the presence of afternoon mist during most of the year.

The water balance for La Planada shows that on average every month has a surplus of water which is lost as soil runoff (Table 2-1). Nevertheless, in some years there might be months in which there is a water deficit. This can explain why during my study period, in particular during the months of July-August of 1993, many plants lost their leaves.

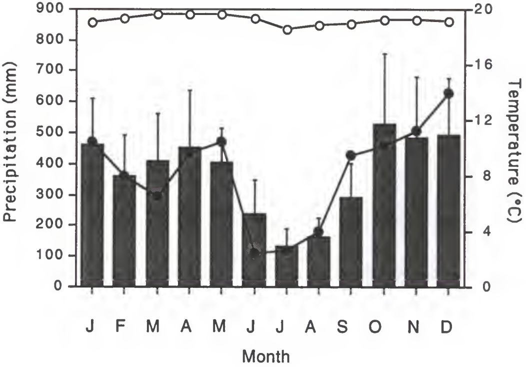


Figure 2-2. Distribution of mean monthly rainfall (bars) and temperature (open circles) (1985-1994) at the Reserva Natural La Planada (unpublished data Reserva Natural La Planada). Filled circles represent average values of rainfall for 1992-1993.

Table 2-1. Water balance for Reserva Natural La Planada, transitional life zone between premontane rain to wet forest (assuming available moisture = 443.7 mm). For details on how to calculate different variables see Ewel and Madríz (1968). Elevation 1,800 m. Based on climatological records from 1985-1995.

		J	F	M	A	M	J	J
Biotemperature	°C	18.9	19.3	19.5	19.6	19.6	19.3	18.5
Potential evapotranspiration (P.ET)	mm	95	88	98	94.8	98	93.4	92.5
Precipitation	mm	460.1	360.7	406.5	451.1	405.3	292.2	148.5
Actual ET	mm	95	88	98	94.8	98	93.4	92.5
Water surplus	mm	365.1	272.7	308.5	356.3	307.3	198.8	56.01
Soil moisture change	mm	0	0	0	0	0	0	0
Moisture available in soil end of month	mm	443.7	443.7	443.7	443.7	443.7	443.7	443.7
All runoff	mm	365	273	309	356	307	199	56
Soil moisture deficit	mm	0	0	0	0	0	0	0
Precipitation deficit	mm	0	0	0	0	0	0	0
Total moisture deficit	mm	0	0	0	0	0	0	0

Table 2-1. (continued)

		A	S	O	N	D	TOTAL
Biotemperature	°C	18.8	18.9	19.2	19.2	19.1	19.2
Potential evapotranspiration (P.ET)	mm	94	91.5	96	92.9	95.5	1129.6
Precipitation	mm	163.2	287.8	527.5	482	491.6	4437.4
Actual ET	mm	94	91.5	96	92.9	95.5	1129.6
Water surplus	mm	69.17	196.3	431.5	389.1	396.1	3347
Soil moisture change	mm	0	0	0	0	0	
Moisture available in soil end of month	mm	443.7	443.7	443.7	443.7	443.7	
All runoff	mm	69.2	196	431	389	396.1	3347
Soil moisture deficit	mm	0	0	0		0	
Precipitation deficit	mm	0	0	0	0	0	0
Total moisture deficit	mm	0	0	0	0	0	

The La Planada forest develops on well drained soils (Dystrandept) derived partially from volcanic material, that are moderately acid, with a sandy to clay loam texture (De Las Salas and Ballesteros 1986). The canopy height (average 22 m) and the basal area (dbh > 4 cm; 33.4 m^2/ha) of the forest are low and epiphytic and hemiepiphytic plants are very abundant (De Las Salas and Ballesteros 1986; Gentry 1988). Plants (dbh > 2.5 cm) in a 0.1 ha plot were represented by 112 species (Gentry 1992a). The most important trees on this plot were Quararibea sp., Elaegia sp., Hieronyma sp., Alchornea sp., Billia colombiana, Inga sp., Otoba sp., and Ocotea sp.; the most important treelets and shrubs were Faramea elegans, Prestoea cf. purpurea, Aiphanes sp., Geonoma weberbaueri, Palicourea gibbosa and Miconia sp.; and the most common epiphytes were Philodendron cf. scandens, Spheraedenia steyermarkii and Psammisia sp. (A. Gentry, unpublished data).

General Sampling Procedure

I chose six sites to evaluate how edge age and distance from the edge towards the forest interior influence various components of fruit production and seed dispersal. These sites, hereafter referred to as edges, were active or recently abandoned pastures contiguous with forest. Thus, at most edges there was a sharp delineation between forest and the adjacent pasture (Table 2-2). Four edges lay at La Planada boundaries (Marcos, Célimo I, Célimo II, and

Hermógenes), a fifth edge was located within the reserve (Pialapí), and the sixth edge was located at El Bosque (Acantayac) (Fig. 2-2). Célimo I and Célimo II were 400 m apart on the same edge, but because of differences in the weeding regime of the pasture and use of the forest I reasoned that they could represent two independent sampling units. Independence of these two sampling points was particularly important for the part of the work evaluating the influence of edges on the distribution of understory birds (Chapter 5). Recapture frequency between these two sites was <4%, supporting the assumption that these two points represented two independent sampling units.

Three edges, Célimo I, Célimo II, and Pialapí, were created around 1950 (old edges), when colonists first arrived in the area and cleared the forest to establish pastures. The other three edges, Marcos, Hermógenges, and Acantayac, were created around 1982 (young edges), the year La Planada was established as a private reserve (Table 2-2). At the beginning of the study, I placed barbed wire fences along the edges to keep cattle from penetrating into the forest. I sampled these edges between March 1992 and March 1994.

At each edge I worked in an area of 100 X 200 m (2 ha) and established four strips (100 X 10 m) running parallel to the edge. These strips were located at four different distances from the forest edge towards the forest interior: 0-10 m (D1), 30-40 m (D2), 60-70 m (D3), and 190-200 m (D4).

Table 2-2. Characteristics of the edges included in this study.

Edge	T[1]	O[2]	A[3]	C[4]	PS[5]	G[6]	CU[7]	FU[8]
Célimo I	S	40° NE	1953	H	6.0	4.2	Cattle ranching; pasture	Extraction of palm hearts and poles; cattle grazing
Célimo II	S	19° NE	1953	M	7.6	7.6	Cattle ranching; pasture	Extraction of palm hearts and poles; cattle grazing
Pialapí	F	8° NE	1950	L		9.9	Trail to Pialapí; second growth	Selective logging 40 yr ago
Acantayac	F	24° NE	1981	M	3.0	11.0	Cattle ranching; pasture	Extraction of palm hearts and poles; cattle grazing; ancient graves
Hermógenes	M	68° NE	1982	H	3.0	10.0	Cattle ranching; pasture	Extraction of palm hearts
Marcos	S	59° NE	1982	H	1.0	7.5	Cattle ranching; pasture	Extraction of palm hearts and poles; cattle grazing; old path to Pialapí

[1] T = Topography; S = steep, M = moderate, F = flat

[2] O = Orientation (position of edges regarding the cardinal points)

[3] A = Age (year the forest was clear cut)

[4] C = Edge contrast; H = high, M = moderate, L = low

[5] PS = Size of disturbed area (ha)

[6] G = Percent of sampling area covered by gaps

[7] CU = Use of clear cut area

[8] FU = Use of forested area

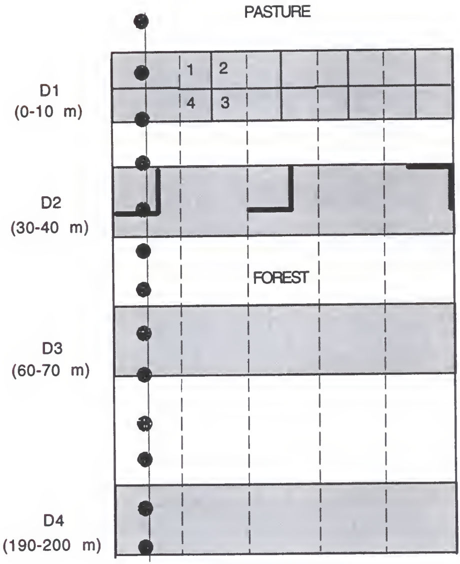


Figure 2-3. Edge indicating general sampling design. Shaded strips represent four distances where sampling took place: D1 (0-10 m), D2 (30-40 m), D3 (60-70 m), and D4 (190-200 m). In strip D1 I show the distribution of subquadrats (1-4) where fruit abundance was evaluated. In strip D2 I show the distribution of each of three pirs of mistnets (perpendicular dark lines). On the left side of the figure I illustrate the orientation of one transect along which LAI was measured.

CHAPTER 3

FROM FLOWERS TO SEEDLINGS: THE EFFECT OF EDGES AND TREEFALL GAPS ON TWO TROPICAL UNDERSTORY PLANTS, *Palicourea gibbosa* AND *Faramea affinis* (RUBIACEAE)

Introduction

Recruitment rates in plant populations are influenced by success at all stages of the life cycle (Harper 1994). Which stages limit recruitment depends on the requirements of individuals at each stage and the spatial distribution of resources (e.g., Sork 1983, Martínez-Ramos and Soto-Castro 1993, Osunkoya et al. 1994). In tropical areas, for example, treefall gaps influence the distribution of resources at small scales (Denslow and Hartshorn 1994), whereas landslides and forest clearings do so at large scales (Guariguata 1990, Dalling and Tanner 1995). Also, seed predation (e.g., Schupp 1988, Schupp and Frost 1989, Samper 1992), seedling establishment (e.g., King 1990), plant growth (Sizer 1992, Dalling and Tanner 1995), fruit production (Levey 1990) and seed dispersal (Murray 1988) change as a result of such disturbances. Little is known, however, about the combined effect of small and large-scale disturbances on the various stages of the life cycle of plants or how such effects may determine which stage limits recruitment.

For the most part, studies evaluating the effect of human disturbances on recruitment rates in tropical plants have focused on single stages of a plant's life cycle (e.g., MacDougall and Kellman 1992, Seizer 1992, Burkey 1993). By looking at several species it has been possible to establish patterns and understand the factors underlying the responses of particular stages (e.g., Sizer 1992). This approach should be complemented with studies focusing on single species to establish the relative contribution of a given stage to the life cycle of a plant (Ellison et al. 1993). A more complete understanding of factors that limit recruitment either in forest fragments or nearby disturbed areas must consider what happens to plants in all stages of their life cycle.

At a neotropical montane site fruiting individuals of *Palicourea gibbosa* and *Faramea affinis* were not distributed uniformly across pasture-forest edges (Chapter 4). Here I report results of a study that examined how several stages of the life cycle of these two understory plants were influenced by distance from forest edge, edge age, and treefall gaps. In particular, I wanted to determine how pollination, fruit set, seed dispersal, seed predation, germination, and seedling growth could result in the observed distribution of *P. gibbosa* and *F. affinis* across the pasture-forest edge.

The Species

Palicourea gibbosa Dwyer and *Faramea affinis* belong to the Rubiaceae, one of the most speciose and common families of neotropical montane forests (Taylor 1989, Gentry 1992*a*). *Palicourea gibbosa* shrubs reach 4 m and are found at middle elevations from Panama to Ecuador (Dwyer 1980; C. Taylor, personal communication), growing in second growth and mature forest (Arias 1993). *Faramea affinis* treelets reach 9 m and grow in old second growth and mature forests. In a 0.1 ha plot at my study site, *P. gibbosa* and *F. affinis* were the most common species (dbh > 2.5 cm) in the understory (A. Gentry, unpublished data).

Palicourea gibbosa exhibits three flowering periods per year. Its yellow flowers are visited mostly by hummingbirds, including *Ocreatus underwoodii*, *Aglaiocercus coelestis*, and *Haplophaedia lugens* (Arias 1993). Fruits of *P. gibbosa* are dark blue to purple, 7 mm long, and are presented in terminal yellow, erect infructescences containing up to 50 fruits. They contain 1-2 seeds, 5.0 x 4.9 mm. *Palicourea gibbosa* seeds are dispersed by birds, including *Myadestes ralloides*, *Pipreola riefferi*, *Atlapetes brunneinucha*, *Masius chrysopterus*, and *Tangara arthus* (C. Restrepo and N. Gomez, unpublished data).

Faramea affinis exhibits two flowering periods per year. Its tubular, purple flowers are visited by hummingbirds, including *Coeligena wilsoni* (Samper 1992). Fruits are blue and are presented in terminal, pendant, green infructescences, containing a maximum of 3 fruits. They measure 20 x 18.2 mm and contain a single seed, 10.4 x 7.6 mm (Samper 1992). Seeds of *F. affinis* are dispersed by a different set of birds, *Andigena laminirostris*, *Lipaugus cryptolophus*, *Pipreola riefferi*, *Semnornis ramphastinus*, and *Trogon personatus* (Restrepo 1990, Beltrán 1991, Samper 1992).

Methods

I evaluated the combined influence of edges and treefall gaps on several stages of the life cycle of *Palicourea gibbosa* and *Faramea affinis* by sampling individuals and conducting experiments at six edges (three old and three new) and at four distances from forest edge towards forest interior (0-10 m, 30-40 m, 60-70 m, and 190-200 m) (Chapter 2). Depending on the stage of the life cycle I was examining, I modified the basic sampling design described in Chapter 2. This was due to logistic constraints, including accessibility of the edges.

Beginning in March 1992 I tagged all individuals ≤ 2 m tall in flower and/or in fruit, and classified them as being in gap or interior. An individual was classified as in gap if it was within a gap (*sensu* Brokaw 1982) or located ≤ 2 m from a gap edge, and as interior if it was located > 2 m from the edge of the nearest treefall gap at the time the study began. I continued tagging individuals throughout the study period as new individuals flowered. For each individual I marked all inflorescences and infructescences and followed them over the entire study period. I monitored individuals for the presence of inflorescences and infructescences on a biweekly basis during the first 6 months (March 1992-August 1992) and on a monthly basis the following 11 months (September 1992-July 1993).

Pollination

To determine the influence of edges on pollination success I looked at pollen tube production. From June 1993 until November 1993 I checked flowering individuals for four consecutive days to collect an average of 10 flowers per individual. These individuals represent a subset of those that were monitored over the 16-month period. I dissected the flowers and fixed the styles in formalin-acetic acid (FAA) to examine pollen tubes. Pollen tubes were stained (Martin 1959, Feinsinger et al. 1992) and counted under an epifluorescent microscope. Styles were processed by P. Amezquita at the Universidad de Santiago de Compostela, Spain. Pollen tube production per individual was expressed as the percentage of flowers with pollen tubes (F) and as the average number of pollen tubes per flower (P).

Fruit Set

For each new inflorescence I counted the number of flower buds and followed them until fruits developed and ripened. I expressed fruit set as the percentage of unripe fruits in relation to the number of flower buds and as the percentage of ripe fruits in relation to the number of unripe fruits counted over the entire study period for each individual. I present results for P. gibbosa only.

Fruit Damage by Insects

At the same time I monitored infructescences for unripe and ripe fruits, I recorded two types of fruit damage by insects: damage to seeds by wasps (Hymenoptera: Chalcidoidea) and removal of pulp by ants (Hymenoptera: Formicidae: Ponerinae). The former could be recognized by exit holes left by newly emerged adults and the latter by bites taken from fruits. These two types of fruit damage were the most common ones for these two understory plants. I expressed seed and fruit damage as the proportion of unripe fruits exhibiting one of the two types of damage in relation to the total number of unripe fruits produced by an individual over the entire study period. I present results for P. gibbosa only.

Seedling Growth and Leaf Production

I monitored seedlings of Palicourea gibbosa and Faramea affinis at each of three distances (0-10, 30-40, 60-70 m) at three old edges (Célimo I, Célimo II, and Pialapí) to establish the combined effect of distance from forest edge and treefall gaps on seedlings growth and leaf production (Fig. 2-1, Table 2-2, Chapter 2). In May 1992 I located seedlings of *P. gibbosa* and *F. affinis*. I placed by their side a stick with a piece of flagging tape with a distinctive number for each seedling. I recorded whether seedlings were growing in treefall gaps ($n = 201$ and $n = 213$, *P. gibbosa* and *F. affinis*, respectively) or intact forest ($n = 210$ and $n = 221$). To standardize measurements I marked the stems of each seedling with yellow vinyl paint (ca. 1.5 cm above soil surface) and the youngest pair of leaves with threads of flagging tape tied around the petioles. With calipers I took a first measurement of the seedling's height from the yellow mark to the base of the meristem and I repeated this procedure five times between May 1992 and October 1993. I also recorded and marked new pairs of leaves.

Seedling growth rate (GR) is expressed as the increment in height between the first (h_n) and the last measurement (h_{n+1}) [$GR = (h_{n+1} - h_n/t_{n+1} - t_n)$*(30 days/month)] (Seizer 1992). Leaf production rate (LPR) is expressed as the number of new leaves produced between the first (l_n) and last (l_{n+1}) period [$LPR = (l_{n+1} - ln/t_{n+1} - tn)$*(30 days/month)].

Field Experiments

Experiments on seed predation and seed germination of *P. gibbosa* and *F. affinis* were performed at three edges (Hermógenes, Célimo I, and Célimo II) and that on fruit removal (*P. gibbosa*) at two edges (Hermógenes and Célimo I) (Fig. 2-1, Chapter 2). Even though these edges represent two different ages (Table 2-1) and edge age is known to influence the effect of distance on vegetation (e.g., Williams-Linera 1990), I chose them to conduct this work because they were close enough to allow frequent monitoring of seeds and fruits. At each of four distances from forest edge (0-10, 30-40, 60-70, and 190-200 m) (Fig. 2-3, Chapter 2) I mapped the treefall gaps and randomly chose 4 of them. At each distance I paired each treefall gap location with an intact forest location.

Seed predation and seed germination

In the seed predation and seed germination experiments I placed an aluminum tray (15 x 7 cm) in each gap and interior site. I punctured the trays to prevent water from accumulating, filled them with soil, and positioned them flush with ground level. I placed 10 seeds of P. gibbosa and 5 seeds of F. affinis in different trays. Seeds were obtained from ripe fruits, and those showing damage by insects were discarded. In total I used 1,920 seeds of P. gibbosa and 960 of F. affinis. I placed 92 trays containing seeds for each edge/species/experiment (32 trays) and simultaneously ran the germination and predation experiments for each species within each edge. The trays containing the seeds sown to evaluate changes in germination rates were covered with galvanized mesh (5 x 5 mm) to protect seeds from vertebrates.

I checked trays on a weekly basis and counted the number of seeds remaining and the number of seeds germinated, i.e., seeds in which the hypocotyyl was visible (ca. 3 mm long). The seed predation experiment for P. gibbosa lasted for 5 days (July 1993-August 1993) and the seed germination experiment for 105 days (July 1993-November 1993). The seed predation experiment for F. affinis lasted for 105 days (August 1993-December 1993) and the seed germination experiment for 252 days (August 1993-April 1994). I concluded the seed germination experiments when 90% of the seeds had germinated and the seed predation experiments when no more seeds were being removed. I assumed that seeds removed from the trays were taken by vertebrates and that this constituted predation.

Fruit removal

In this experiment I placed eight artificial shrubs per distance, 4 at each gap and interior site, for a total of 32 artificial shrubs per edge. Each shrub consisted of a 1.5-m-tall bamboo stick to which I attached an artificial infructescence resembling that of P. gibbosa. The artificial infructescences consisted of a 15-cm-long wooden rod from which four pairs of tooth picks extended. The rods and tooth picks were dyed bright yellow, and at the end of each tooth pick I inserted a recently collected ripe fruit of P. gibbosa. I ran the fruit removal experiment at each edge for four consecutive days. On the morning of the first day (0700) I inserted fresh fruits of P. gibbosa and 24 hours later recorded the number of fruits missing and bitten by ants. All fruits were changed every 24 hours to start a new run of the experiment. I ran this experiment from June 26 1993 to July 3 1993.

Analyses

I analyzed data with ANOVAs for Mixed Factorial designs (Girden 1992). The full design (edge age, distance from forest edge, and treefall gaps) was set up as a split-split-plot design (Winer et al. 1991). The factors of interest were edge age, distance from the edge, and habitat. The edges that I sampled for each level of edge age (old and new) were chosen at random and represented the plot unit. In turn, each edge was divided into four strips (distances from the forest edge towards the forest interior) representing the subplot units. Randomization of the levels of the distance factor was restricted but because the strips were separated in space and I analyzed responses from nonmobile organisms I assumed they represented independent subsampling units. Finally, individuals were classified according to habitat as gap or intact forest, the latter representing the sub-subplots.

The design for the seed predation, seed germination, and fruit removal experiments was set up as a split-plot design with one repeated measure (Winer et al. 1991). The factors of interest were distance from the edge, habitat, and time, with time being the repeated measure. In the seed predation-seed germination and fruit removal experiments time was represented by weeks and days, respectively. In my design distance (D1 to D4) represents the plot unit, habitat (gap and intact forest) the subplot unit, and edges replicates.

The number of individuals within the gap and interior categories differed at each distance/edge, producing an unbalanced design. I used Type III SS, since it takes into account differences in cell frequencies between treatment combinations (Gagnon et al. 1989; Potvin 1993). To determine whether data satisfied assumptions of an ANOVA, I plotted residuals as a function of fitted Y values. When residuals where not normally distributed, I transformed the data (see type of transformation for each data set).

In all cases, I used an alpha of 10% to increase power of the tests (Zolman 1993). I did so for several reasons. First, the scale at which I worked precluded inclusion of more replicates, which is often the case when dealing with large-scale ecological phenomena (Scheiner 1993). The area encompassed by the six edges was equivalent to 12 ha and access to them was difficult due to steep terrain. Second, in a mixed factorial design the number of degrees of freedom is reduced compared to a factorial design because of multiple nesting (Zolman 1993). In the field, I was limited by the number of edges I could reach within walking distance from the field station, thus I had to set up the design as described. Lastly, the use of Type III SS to analyze unbalanced data sets may lead to Type II errors (Potvin 1993). By increasing the probability of alpha, I compensate for this bias, although it consequently increases Type I errors. In all cases I present P-values.

Results

Pollen Tubes

Distance from forest edge did not influence the production of pollen tubes in Palicourea gibbosa and Faramea affinis (Table 3-1 and Table 3-2). The percentage of flowers with pollen tubes and the average number of pollen tubes per flower in P. gibbosa, however, was influenced by edge age (ANOVA, $F_{1,4} = 9.2$, $P = 0.04$ and $F_{1,4} = 7.7$, $P = 0.05$, respectively, Table 3-1). At old edges individuals had a higher percentage of flowers with pollen tubes and more pollen tubes per flower (50% ± 3.1% and 2.7 ± 0.3, n = 105, mean ± SE, respectively) than those at new edges (36% ± 4.8% and 2.3 ± 0.5, n = 52, respectively).

Habitat influenced the percentage of F. affinis flowers with pollen tubes and the number of pollen tubes per flower (ANOVA, $F_{1,4} = 8.0$, $P = 0.02$ and $F_{1,4} = 11.8$, $P = 0.01$, respectively, Table 3-1). In intact forest individuals had a higher percentage of flowers with pollen tubes and more pollen tubes per flower (32.5% ± 3.3% and 0.7 ± 0.06, mean ± SE, n = 81, respectively) than those in gaps (26.0% ± 3.1% and 0.5 ± 0.07, n = 48, respectively). The effect of habitat, however, was modified by edge age and distance from forest edge as shown by the significant interaction of

Table 3-1. Results of ANOVAs for Mixed Factorial Designs (Split-split-plot) on percentage of flowers with pollen tubes in relation to the total number of flowers (F) and average number of pollen tubes per flower (P) for *Palicourea gibbosa* and *Faramea affinis*. Significance at 10% (*),5% (**), and 1% (***).

Variable	Age A		Edge(A) Error		Distance D		D x A		DxE(A) Error	
	df	F	df	SS	df	F	df	F	df	SS
P. gibbosa										
F	1	9.2**	4	8011.5	3	0.5	3	1.3	12	11229.4
P	1	7.7**	4	35.6	3	0.3	3	2.5	12	49.9
F. affinis										
F	1	3.9	4	2408.8	3	0.2	3	0.5	12	5054.8
P	1	1.9	4	1.9	3	0.4	3	0.5	12	3.6
	Habitat H		H x D		H x A		H x D x A		Hx[E(A)xD] Error	
	df	F	df	F	df	F	df	F	df	SS
P. gibbosa										
F	1	1.0	3	0.5	1	0.4	3	0.17	16	8968.1
P	1	4.1	3	1.4	1	0.3	3	0.3	16	65.04
F. affinis										
F	1	8.0**	3	1.2	1	0.09	3	2.6	16	1239.6
P	1	11.8***	3	0.9	1	2.4	3	4.3**	16	0.9

Table 3-2. Proportion of flowers with pollen tubes in relation to the total number of flowers (F) and average number of pollen tubes per flower (P) in _Palicourea gibbosa_ and _Faramea affinis_ in relation to distance from forest edge. Numbers are the mean ± standard error and number of individuals sampled ().

	D1	D2	D3	D4
Palicourea gibbosa				
F	43.3 ± 4.0	35.7 ± 7.6	52.5 ± 5.0	43.0 ± 6.4
	(59)	(19)	(52)	(27)
P	2.7 ± 3.5	2.1 ± 3.7	2.8 ± 2.9	2.4 ± 2.9
Faramea affinis				
F	28.7 ± 3.3	25.0 ± 3.7	35.2 ± 5.1	33.3 ± 3.6
	(n=39)	(n=29)	(n=24)	(n=37)
P	0.6 ± 0.08	0.4 ± 0.08	0.7 ± 0.1	0.6 ± 0.09

habitat, distance, and edge age (ANOVA, $F_{3,7} = 4.3$, $P = 0.05$, Table 3-1).

Fruit Set

In *Palicourea gibbosa* fruit set was influenced by distance from forest edge, but the effect depended on edge age, as shown by the significant interaction between distance and edge age (ANOVA, $F_{2,2} = 5.8$, $P = 0.02$, Table 3-3). At D1 and D2 the percentage of developing fruits was greater at new than at old edges but this trend was reversed at D3 where 28% ± 0.02% (mean ± SE) of the flower buds resulted in fruits in old edges as compared to 20.0% ± 0.02% in new edges (Fig. 3-1). The percentage of ripe fruits was also influenced by distance and similarly depended on edge age (ANOVA $F_{2,2} = 3.9$, $P = 0.06$, Table 3-3). At D1 and D3 the percentage of ripe fruits was greater at new edges but the trend was reversed at D2. At D2 in old edges, 51.0% ± 0.05% of fruits ripened compared to 42.0 ± 0.04% at new edges (Fig. 3-1).

Seed and Fruit Damage

The percentage of *Palicourea gibbosa* fruits damaged by ants and wasps did not differ among the four distances (Table 3-3). Edge age, however, influenced the percentage of fruits eaten by ants but depended on habitat as shown by the significant interaction between edge age and habitat (ANOVA, $F_{1,1} = 4.0$, $P = 0.07$, Table 3-3). At new edges, individuals growing in gaps had a higher percentage of fruits damaged

Table 3-3. Results of ANOVAs for Mixed Factorial Designs (Split-split-plot) on percentage of fruit set (UF/FB), percentage of fruits ripening (RF/UF), percentage of seeds damaged by wasps (UFW/FV), and percentage of fruits damaged by ants (UFA/FV) in Palicourea gibbosa. °
Log-transformed data. Significance at 10% (*),5% (**), and 1% (***).

Variable	Age		Edge(A)		Distance		D x A		DxE(A)	
	A		Error		D				Error	
	df	F	df	SS	df	F	df	F	df	SS
UF/FB°	1	0.0	4	0.1	3	2.8	3	5.8**	12	0.001
RF/UF	1	1.0	4	0.5	3	0.0	3	3.9**	12	0.9
UFW/FV	1	0.0	4	0.001	3	1.4	3	0.5	12	0.002
UFA/FV	1	0.0	4	0.2	3	0.5	3	1.6	12	0.6

	Habitat		H x D		H x A		H x D x A		Hx[E(A)xD]	
	H								Error	
	df	F	df	F	df	F	df	F	df	SS
UF/FB	1	4.7*	3	0.9	1	1.8	3	1.1	16	0.05
RF/RF	1	1.7	3	0.4	1	0.1	3	0.4	16	1.7
UFW/FV	1	0.001	3	0.7	1	0.3	3	0.3	16	0.003
UFA/FV	1	1.2	3	1.4	1	3.9*	3	1.7	16	4.2

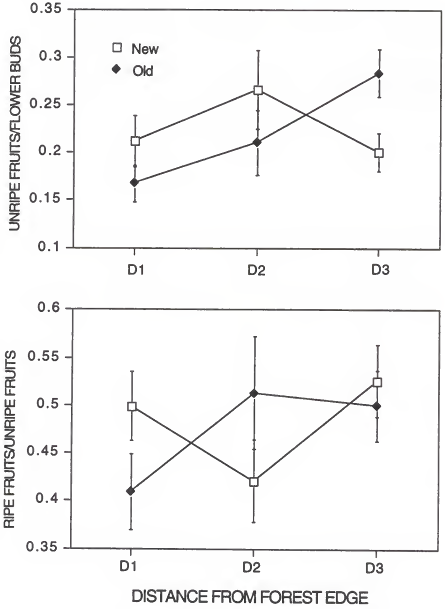


Figure 3-1. Fruit set in *Palicourea gibbosa* as influenced by distance from forest edge. Points are means and bars standard errors.

by ants (7% ± 0.01%, mean ± SE) compared to intact forest (3% ± 0.01%). This trend was reversed at old edges.

Fruit Removal

Even though on average more fruits of Palicourea gibbosa fruits were removed from the artificial infructescences at D2 (0.4 ± 0.2, mean ± SE) than at the other distances (D1, 0.3 ± 0.09, D3, 0.3 ± 0.9, and D4, 0.1 ± 0.08), this difference was not significant (ANOVA, $F_{3,3} = 0.4$, $P = 0.7$). The same was true for habitat where on average more fruits were removed from intact forest (0.3 ± 0.1) than from gaps (0.2 ± 0.06) (ANOVA, $F_{1,52} = 0.6$, $P = 0.4$).

Seed Predation

The number of seeds remaining in the trays averaged over time did not differ among the four distances in Palicourea gibbosa but they did differ in Faramea affinis (ANOVA, $F_{3,6} = 3.5$, $P = 0.09$; Table 3-4, Fig. 3-2a). In F. affinis the number of seeds remaining in the trays decreased from D1 to D4, indicating higher removal rates at the interior. Habitat alone did not have an effect on the number of seeds remaining in the trays for either species (Table 3-4, Fig. 3-3a).

In F. affinis the distance effect was modified by habitat and by week as shown by the significant distance x habitat and distance x week interactions (ANOVA, $F_{3,80} = 2.3$, $P = 0.08$ and $F_{51,102} = 2.0$, $P = 0.002$, respectively, Table 3-4). The number of F. affinis seeds remaining in the trays was similar in gap and intact forest from D1 to D3, but lower in gap (3.5 ± 0.1, mean ± SE) than in intact forest at D4 (4.4 ± 0.08). Over the 18-week period the mean number of F. affinis seeds remaining in the trays decreased at all four distances but the rate of decline was steeper at D4 and at D2 than at D1 and D3.

Seed Germination

Palicourea gibbosa seeds germinated sooner (week 6) than Faramea affinis seeds (week 18). Averaging over time, germination rates of P. gibbosa seeds were significantly affected by distance from forest edge. The same was not true for F. affinis. Germination rates of P. gibbosa seeds were greater at D2 than at D1 and D4 (ANOVA, $F_{3,6} = 5.0$, $P = 0.04$; Table 3-4, Fig. 3-2b). Habitat had a significant effect on seed germination rates in P. gibbosa but not in F. affinis (ANOVA, $F_{1,80} = 7.3$, $P = 0.008$ and $F_{1,78} = 2.3$, $P = 0.13$, respectively). Averaged over time, more seeds of P. gibbosa germinated in gaps than in intact forest (Fig. 3-2b).

The effects of distance and habitat were modified by time as shown by the significant distance x week (F. affinis) and habitat x time (P. gibbosa) interactions (ANOVA, $F_{42,84} = 2.0$, $P = 0.003$ and $F_{3,1120} = 20.3$, $P = 0.006$, respectively). In the former, germination rates over time were steeper at D2 and D3 than at D1 and D4. In the latter, germination rates were higher at gaps than in intact forest.

Seedling Growth Rate

Distance did not influence relative growth rates in Palicourea gibbosa and Faramea affinis (Table 3-5, Fig. 3-2c). Habitat, however, had a major effect on both species (Table 3-5). Seedlings showed greater growth rates (ANOVA, P. gibbosa, $F_{1,399} = 38.7$, $P = 0.0001$ and F. affinis, $F_{1,422} = 8.1$, $P = 0.005$; Fig. 3-3c) in gaps than in intact forest. Overall seedlings of P. gibbosa grew faster (5.0 ± 0.17 mm/month, mean ± SE, n = 411) than those of F. affinis (2.4 ± 0.08 mm/month, mean ± SE, n = 434).

Leaf Production

As with growth rate, habitat and not distance from forest edge had a significant effect on leaf production (ANOVA, P. gibbosa, $F_{1,408} = 17.1$, $P = 0.0001$ and F. affinis, $F_{1,424} = 3.4$, $P = 0.06$; Table 3-5, Figs. 3-2d, 3-3d). Seedlings of both species produced more leaves per month in gaps than in intact forest (Fig. 3-3d). Overall, leaf production was greater in seedlings of Palicourea gibbosa (0.8 ± 0.01 pairs of leaves/month, mean ± SE, n = 420) than in seedlings of Faramea affinis (0.38 ± 0.008 pairs of leaves/month).

Discussion

Of the stages of a plant's life cycle, I examined pollination, fruit set, seed dispersal, seed predation, seed germination, and seedling growth. An important stage

Table 3-4. Results of Mixed Factorial ANOVAs (Split-splot, 1 repeated measure) on mean numbers of seeds remaining in trays (predation experiment) and mean number of seeds germinated in trays (seed germination experiment) for *Palicourea gibbosa* (PG) and *Faramea affinis* (FA). Significant at 10% (*),5% (**), 1% (***), 0.1% (****)

	Distance		D x E		Habitat		H x D		TxHx(DxE)] Error	
	df	F	df	SS	df	F	df	F	df	SS
FA (Predation)	3	3.5	6	75.4	1	1	3	2.3*	80	1068.9
PG (Predation)	3	0.3	6	182.7	1	1.5	3	1.9	80	2721.1
FA (Germination)	3	0.1	6	19.9	1	2.3	3	0.5	78	366.8
PG (Germination)	3	5.0**	6	24.2	1	7.3***	3	1.6	80	910.6

	Week x D		W x D x E		Week		W x H		W xH x D		W x T x[Hx(DxE)]	
	df	F	df	SS	df	F	df	F	df	F	df	SS
FA (Predation)	51	1.9***	102	50.9	17	44.2****	17	1.7	51	1.3	1360	769.2
PG (Predation)	15	0.3	30	60.6	5	163.7****	5	1.4	15	1.6	400	845.4
FA (Germination)	70	2.7***	210	71.4	35	304.4****	35	1.2	105	0.6	2730	907.2
PG (Germination)	42	2.0**	84	87.8	14	835.0****	14	4.3***	42	0.9	1120	1300.5

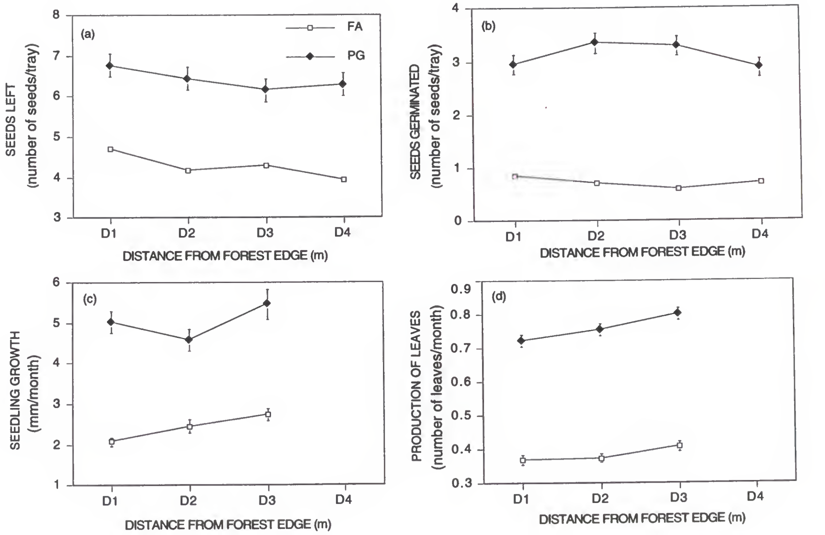


Figure 3-2. Seed germination (a), seed predation (b), seedling growth (c), and leaf production in *Palicourea gibbosa* and *Faramea affinis* as influenced by distance from forest edge. Points represent means and bars standard errors.

missing from this analysis is seedling establishment which links seed germination to seedling growth. In discussing my results I assume that all seeds that germinated survived into the seedling stage. I also restrict this discussion to those stages for which I present results for both *Palicourea gibbosa* and *Faramea affinis*.

Fruiting individuals of *P. gibbosa* and *F. affinis* were not distributed uniformly from pasture to forest interior (Chapter 4). *Palicourea gibbosa* was more abundant closer to the forest edge (D1-D3) than farther inside the forest (D4), and *F. affinis* was more abundant at D2 and D3 than at D1 and D4 (Chapter 4). Such distributions suggest that distance from forest edge influences one or more stages in the life cycle of these plants. My results show that not all stages in the life cycle of *P. gibbosa* and *F. affinis* are influenced equally by the creation of edges and treefall gaps. In addition, species differed in their response to these two types of disturbance.

Pollination was influenced by habitat and edge age but not by distance from forest edge. The percentage of flowers with pollen tubes and the average number of pollen tubes per flower decreased from intact forest to gaps (*F. affinis*) and from old edges to new edges (*P. gibbosa*). Although edges and treefall gaps represent two different scales of disturbance, results for these two species suggest that recently disturbed areas affect pollination levels. My results regarding the effect of distance on pollination levels are similar to those

Table 3-5. Results of Mixed Factorial ANOVAs (Split-splot, 1 repeated measure) on relative growth (mm/month) and relative leaf production (pairs of leaves/month) rates in *Palicourea gibbosa* (PG) and *Faramea affinis* (FA). Significant at 10% (*),5% (**), 1% (***), 0.1% (****).

	Distance		D x E		Edge		Habitat		H x D		Residual	
	df	F	df	SS	df	F	df	F	df	F	df	SS
FA (Growth)	2	3.3	4	19.4	2	0.9	1	8.1***	2	2	422	1053.7
PG (Growth)	2	0.2	4	421	2	1.7	1	38.7****	2	1.1	399	4101.1
FA (Leaves)	2	1.1	4	0.2	2	5.2***	1	3.4*	2	0.7	424	10.3
PG (Leaves)	2	0.5	4	1.4	2	2.1	1	17.1****	2	1.2	408	16

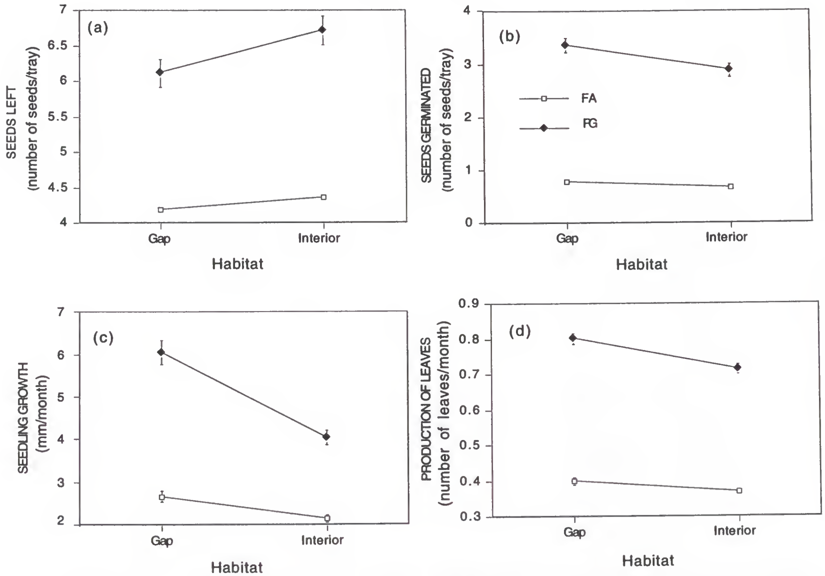


Figure 3-3. Seed germination (a), seed predation (b), seedling growth (c), and leaf production in _Palicourea gibbosa_ and _Faramea affinis_ as influenced by habitat. Points represent means and bars standard errors.

reported by Murcia (1993) for a Colombian site north of La Planada. She found that pollination levels in 11 out of 13 species were not affected by distance from forest edge and explained these results in terms of hummingbirds not being influenced by edges. At La Planada I found that this was the case (Chapter 5). Mean capture rates of nectarivorous birds were not influenced by distance from forest edge. It seems then that pollination can not account for differences in the distribution of fruiting individuals of P. gibbosa and F. affinis across pasture-forest edges.

Seed predation increased from edge towards forest interior in F. affinis but not in P. gibbosa. The effect of distance from edge on F. affinis, however, was influenced by time. Not only were more seeds removed at D4 but they were removed faster than at the other distances. In both species, seed germination was affected by distance from forest edge but depended on time. Seeds closer to the edge germinated sooner than those in forest interior. Assuming an equal probability of seeds arriving at any of the four distances, it is likely that seed predation and seed germination may limit recruitment rates in these two species across pasture-forest edge. Differences in seed predation (F. affinis and P. gibbosa) and in seed germination (F. affinis) over time may result in fewer individuals of these two species establishing in the forest interior (D4).

In another study of F. affinis conducted at La Planada Samper (1992) found that (1) seed removal rates were not affected by habitat (gaps, edge of gaps, and intact forest), (2) seed germination rates were faster in gaps (mean = 174 days, n = 148) than along edges of treefall gaps (177, n = 132) and intact forest (187, n = 135), and (3) seedling establishment (i.e., the stage at which seedlings become independent from food reserves contained in the seeds) was not affected by habitat. Samper's work and mine show that the seed and seedling stages in F. affinis are affected differently by treefall gaps and edges resulting from human activities.

Once seeds of P. gibbosa and F. affinis arrive and germinate at any distance from forest edge, treefall gaps seem to have a major influence on these two species by increasing growth and leaf production rates in seedlings. This is not in accordance with results obtained in the Amazon, where relative growth rates of seedlings was greater up to 10 m from forest edge towards forest interior (Seizer 1992).

My study shows that edges can influence recruitment rates of P. gibbosa and F. affinis through their effect on seed predation and seed germination but not on pollination and the growth of seedlings. On the other hand, treefall gaps influence recruitment rates through their effect on seedling growth.

CHAPTER 4

UNDERSTORY FRUIT ABUNDANCE IN A NEOTROPICAL MONTANE FOREST: THE INFLUENCE OF EDGES AND TREEFALL GAPS

Introduction

Fruit abundance can be influenced by disturbances occurring at various scales. In general, fruit abundance increases in small, natural disturbances, such as treefall gaps (Blake and Hoppes 1986; Levey 1988a,b), in large, natural disturbances, such as patches affected by hurricanes (Walker and Neris 1993) or fire (Fleming 1988), and in large, human-disturbed areas, such as abandoned fields and pastures (Martin 1985; Levey 1988a,b; Blake and Loiselle 1991; Lugo and Frangi 1993; but see Wong 1986). In treefall gaps high fruit production is the result of an increase in the number of fruits produced by individuals growing in the disturbed area compared to conspecifics growing in intact forest and to an increase in the number of fruiting individuals (Piñero and Sarukhan 1982; Clark and Clark 1987; Levey 1990). In large disturbed areas, high fruit production has been related to the same two factors (Auclair and Cottam 1971; Halls 1973; McDiarmid et al. 1977; Fleming 1988), and to the appearance of pioneer species that typically produce more fruits than late successional or mature-forest species (Martin 1985).

It has been suggested that the spatial heterogeneity of the fruit resource base, regardless of the scale at which disturbances occur, influences the distribution of organisms feeding on fruits (e.g., Martin 1985; Wong 1986; Levey 1988a,b; Heideman 1989; Blake and Loiselle 1991; Loiselle and Blake 1991) and the resulting dispersal of seeds (Murray 1988). Nevertheless, depending on the scale of disturbance changes in seed dispersal might have different consequences for the plants. For example, small-scale disturbances may influence recruitment within populations whereas large-scale disturbances may influence colonization of new areas (Harper 1994).

One immediate consequence of disturbance is the creation of edges or boundaries. In general, boundaries mediate fluxes between adjacent ecological systems (Margalef 1968; Wiens et al. 1985; Gosz 1991). Moreover, because of differences in their permeability to fluxes of material and energy, boundaries may influence the dynamics of neighboring systems (Correll 1991; Ryszkowski 1992). In this context, edges that bound patches resulting from disturbance might influence the dynamics and structure of the neighboring patches by influencing the distribution of resources and/or movement of organisms (Crist et al. 1992; Johnson et al. 1992; Wiens 1992). In particular, edges resulting from large-scale disturbances may influence the movement of seeds and thus the structure of whole landscapes.

Seed movement and fruit abundance are related in at least two ways. First, fruit numbers determine the availability of seeds. Second, fruit and seed availability affect the behavior of the dispersers (Murray 1987; Loiselle and Blake 1993). In spite of these well known relationships between fruit abundance and seed movement, few studies have addressed how edges influence fruit abundance (Blanchard 1992). I explored this question in the understory of a neotropical montane forest using edges resulting from forest clear-cutting. In particular, I documented how fruit abundance and seed movement were affected by distance from the forest edge towards the forest interior for the assemblage of understory shrubs and for individual species. Since edge age (Williams-Linera 1990; Blanchard 1992) and treefall gaps (Janzen 1983; Lovejoy et al. 1986; Noss 1991) can modify the steepness of such a response, I examined how they interacted with distance. By looking at four different scales, edges of different age within the forest matrix, distance from forest edge within edges, treefall gaps and foliage density (LAI) within each distance, I could examine changes in the fruit resource base along edges resulting from large-scale disturbances.

Methods

Canopy Structure

I estimated leaf area index (LAI) (m^2 foliage area/m^2 ground area) to (1) characterize the structure of the forest canopy across the pasture-forest edge and to (2) relate LAI to fruit abundance. Fruit production is strongly influenced by light environment (e.g., May and Antcliff 1963; Jackson and Palmer 1977), which in the subcanopy and on the forest floor is influenced by canopy structure (Norman and Campbell 1991). Thus LAI estimates provide a fine-scale description of the light environment of each point where I sampled fruits.

I used a LAI-2000 Plant Canopy Analyzer (Li-Cor, Inc.) in October 1993 to estimate LAI at the three old edges. Estimates of LAI obtained with this instrument are based on the transmitted fraction of incident radiation on the canopy. At each of the old edges (Célimo I, Célimo II, and Pialapí) I established three transects running perpendicular to the forest edge and extending 10 m into the pastures and 210 m into the forest (Chapter 2, Fig. 2-3). I made readings at intervals of 5 m in the first 50 m of the transect, 10 m in the next 130 m, and 20 m in the next 40 m. For each point along a transect I made four consecutive below-canopy readings that together were paired with a single reading taken in an area devoid of trees and shrubs in the nearby pasture. I always kept the lens and LAI-2050 optical sensor pointing in the same direction and 1.5 m above the ground. I covered the optical sensor with a 45° view cap to block my image and direct beam radiation during clear days (Li-Cor 1992).

Estimates obtained with this instrument often underestimate true LAI (Chason et al. 1991; Hannan and Bégué 1995). Nevertheless, in the context of this study these values are useful to describe relative changes in canopy structure across the pasture-forest edge.

Fruit Abundance

To establish the influence of edges and treefall gaps on fruit production by understory plants I subdivided each of the four 100 x 10 m strips within each edge into five 20 x 10 m quadrats (Chapter 2, Fig. 2-3). In turn each quadrat was subdivided into four 10 x 5 m subquadrats and for each quadrat I chose at random two subquadrats in which to monitor fruit production (Fig. 2-3).

I used Brokaw's (1982) definition of treefall gap to classify each subquadrat as gap or interior habitat. A subquadrat was classified as gap if it was within a gap or located <5 m from a gap edge, and as interior if it was located ≥5 m from the edge of the nearest treefall gap at the time the study began. These two categories do not reflect the environmental continuum from the center of the treefall to the intact forest nor do they take into account differences in gap size and shape (Brown 1993; Denslow and Hartshorn 1994). Nevertheless, I was more interested in the possible interaction between distance from the edge and treefall gaps than in the treefall gaps themselves.

I monitored changes in fruit production at each pair of the 10 x 5 m subquadrats over a 12 mo period (September 1992-August 1993, excluding December). In each subquadrat I identified and counted individual plants $\leq$7 m tall bearing unripe and/or ripe fleshy fruits (Levey 1988a,b; Blake and Loiselle 1991). I also included broken limbs bearing fruits. Most species I recorded complete their life cycle within this arbitrarily set understory stratum. A few species, mostly in the Arecaceae (palms), Rubiaceae, and Melastomataceae, also fruit in higher strata. For each individual, except species in the Araceae, I counted the total number of unripe and ripe fruits every month on a biweekly basis. I averaged these biweekly counts to obtain a single value on fruit abundance for any given month.

I expressed fruit production in four different ways: (1) total number of individuals bearing unripe and/or ripe fruits (TI); (2) total number of fruits (unripe + ripe fruits) (TF); (3) total number of ripe fruits (RF), and (4) total number of fruits (unripe + ripe fruits), excluding the Arecaceae (TF-A). In all cases, fruit abundance is expressed as the mean number of counts per 50 m^2, the area of each 10 x 5 m subquadrat.

I included unripe fruits because they constitute a food resource for frugivorous insects. I excluded the Araceae from variables 2-3 because it was difficult to estimate fruit numbers for each infructescence. I excluded the Arecaceae from variable 4 because their high productivity and prolonged fruiting season could mask patterns of fruit production among shrubs producing fewer fruits and fruiting over shorter periods of time.

To explore fruit abundance responses to edges at the species level I looked at the number of individuals bearing unripe and/or ripe fruits. For each species I pooled this information for all subquadrats and months to obtain a single value for each edge age and distance.

I collected most plant species and deposited voucher specimens at Botany Department Herbarium, Arizona State University (ASU), Herbario Nacional de Colombia (COL), Botany Department Herbarium, Field Museum of Natural History, Chicaco (F), Herbario de la Universidad de Antioquia (HA), Kew Botanical Garden (K), Missouri Botanical Garden (MO), New York Botanical Garden (NY), Herbario Universidad de Nariño (PSO), Utrecht Herbarium (U), Smithsonian Institution (US), and Department of Botany Herbarium, University of Wisconsin (WIS). Family names follow Cronquist (1981).

Seed Movement

To evaluate seed movement across edges I counted and identified seeds contained in bird droppings retrieved from birds captured in mist nets. Birds were sampled at the same edges and distances from the forest edge as were fruiting plants (Chapter 5). After capture, birds were kept in cloth bags lined with filter paper for ca. 20 min. Bird droppings were preserved in alcohol and seeds were compared to a reference collection, compiled during the study period.

This method for evaluating seed movement may have biases in addition to those involved when sampling birds with mist nets (see Chapter 5). In particular, seeds recovered from birds might represent a non-random sample of seeds ingested, since seed handling varies within and among species depending on seed size and other seed characteristics (Levey 1986, 1987). Nevertheless, this method does provide information on seed movement that would be difficult to determine by other means (e.g., seed traps).

Analyses

I used a Repeated Measures ANOVA to analyze LAI. Edge was included as a between factor variable, distance from the edge as a within factor variable, and individual transects as subjects.

I analyzed data on fruit production at the community level with ANOVAs for mixed factorial designs (Girden 1992). The mixed design was set up as a split-split-plot design with one repeated measure (Winer et al. 1991). The factors of interest were edge age, distance from the edge, habitat, and month, the latter representing the repeated measure. The six edges that I sampled for each level of edge age (old and new) were chosen at random from a population of old and new edges and represented the plot unit. In turn, each edge was divided into four strips, i.e., distances from the forest edge towards the forest interior, representing the subplot units. Randomization of the levels of the distance factor was restricted, but because the strips were separated in space and I analyzed responses from non-mobile organisms I assumed they represented independent subsampling units. This was supported by results of an ANOVA in which distance was included as a repeated measure and the epsilon factor equaled one, indicating no correlation between the levels of the distance factor (Girden 1992). Finally, fruit production was monitored in subquadrats that were chosen at random and classified according to habitat as gap or interior, the latter representing the sub-subplots.

The number of subquadrats falling within the gap and interior categories differed at each distance among the edges, producing an unbalanced design. I used Type III SS since it takes into account differences in cell frequencies between treatment combinations (Gagnon et al. 1989; Potvin 1993).

To determine whether the data satisfied assumptions of an ANOVA, I plotted residuals as a function of fitted Y values. When residuals where not normally distributed, I log-transformed the data. In addition, I verified the assumption of compound symmetry for the repeated measure factor and used a corrected F-ratio (H-F) to interpret the analyses (Girden 1992; von Ende 1993).

I used an alpha of 10%. I set alpha at this level because my design could lead to increases in Type II errors (reduced power of my tests) (Zolman 1993). Concomitantly I increased the probability of committing Type I errors. First, the scale at which I worked precluded inclusion of more replicates, which is often the case when dealing with large-scale ecological phenomena (Scheiner 1993). The area encompassed by the 6 edges was equivalent to 12 ha and the access to them was difficult due to steep terrain. Second, in a mixed factorial design the number of degrees of freedom is reduced compared to a factorial design because of multiple nesting (Zolman 1993). In the field, I was limited by the number of edges I could reach within walking distance from the field station and thus I had to set up the design as was described above. Lastly, the use of Type III SS to analyze unbalanced data sets may lead to Type II errors (Potvin 1993).

I analyzed fruit abundance data for understory species using a Replicated Goodness of Fit Test (G-statistic) (Sokal and Rohlf 1981) to establish whether distance and edge age affected the number of fruiting individuals. First, I pooled the data for old and new edges and calculated G_P (G-Pooled) to determine if the number of individuals across the four distances departed significantly from a uniform distribution. Second, I compared old and new edges and calculated G_H (G-

Heterogeneity) to test for homogeneity between the two edge ages. For these two analyses I used only species in which at least 80 percent of the expected cell frequencies were greater than 5, since the G statistic departs from the χ^2 distribution if this is violated (Siegel and Castellan 1988).

Results

LAI and Distance from the Edge

I measured LAI only at old edges and found that major changes in LAI were observed at the interface between pasture and forest (Fig. 4-1). Once inside the forest, LAI values were highly variable not only from the edge towards forest interior but also among edges at the same distance (Fig. 4-1). Averaging over the three edges, variability in LAI measurements for the 0-40 m interval (Coefficient of variation, CV = 0.3) was identical to that for the 50-210 m interval (CV = 0.3).

I did not include pasture LAI values in the ANOVA to establish the effect of distance on LAI. LAI did not differ significantly either among edges (ANOVA, $F_{3,5} = 0.4$, $P = 0.75$) or in relation to distance from the forest edge towards the forest interior ($F_{23,\ 115} = 0.47$, $P = 0.98$) (Table 4-1). This indicates that at least along old edges, canopy structure does not vary in a predictable way from the edge towards the forest interior.

LAI and Fruit Abundance

To establish whether LAI influences fruit abundance, I averaged values of fruit abundance for each pair of 50 m^2 subquadrats where I took LAI measurements. LAI was not significantly correlated with total number of fruits (TF) (Coefficient of determination, $r^2 = 0.032$, n =36), total number of fruits excluding the Arecaceae (TF-A) ($r^2 = 0.077$, n = 36), total number of ripe fruits (RF) ($r^2 = 0.015$, n = 36), or total number of fruiting individuals (TI) ($r^2 = 0.02$, n = 36) (Fig. 4-2).

Fruit Abundance

Plant Assemblages

In the ANOVAs none of the three-way interactions was significant. Several two-way interactions were significant but not consistently so for the four measurements of fruit abundance. In describing the results I look first at the single effect of distance on fruit abundance and then at the interactions involving this term.

The total number of fruits (TF) and total number of ripe fruits (RF) differed significantly among the four distances on a yearly basis (ANOVA, $F_{3,12} = 4.3$, $P = 0.03$ and $F_{3,12} = 5.4$, $P = 0.01$, respectively) (Table 4-2). For TF and RF the mean number of fruits as well as the variance decreased from forest edge towards forest interior (Fig. 4-3). There are three not mutually exclusive explanations for these results.

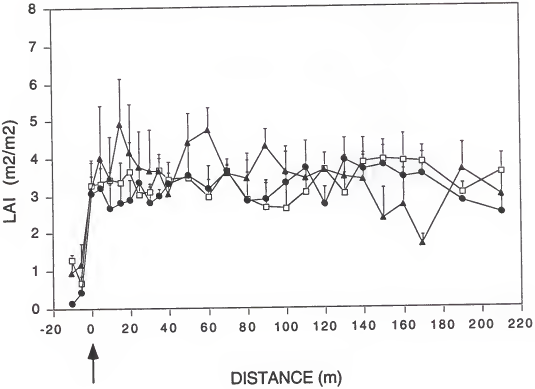


Figure 4-1. Leaf area index across the pasture-forest edge, indicated by the arrow (0 m). Points represent the average of three measurements per edge and bars the standard errors. Open squares = Pialapí, open triangles = Célimo II, and filled circles = Célimo I.

Table 4-1. Results of a Mixed Factorial ANOVA on leaf area index for old edges at the Reserva Natural La Planada

Source	df	SS	MS	F-Value	P-Value	H-F
Edge	3	6.768	2.256	0.401	0.7585	
Transect (Edge)	5	28.095	5.619			
Distance	23	11.64	0.506	0.468	0.981	0.981
Distance * Edge	69	76.934	1.115	1.031	0.4367	0.437
Distance * Transect (Edge)	115	124.376	1.082			
		H-F Epsilon				
Distance		1.714				

First, individuals growing at D1 (0-10 m) produced more fruits than those growing at other distances. Support for this comes from the fact that distance did not have an effect on the total number of fruiting individuals (TI) (Table 4-2) and the observation that some species that were heavily represented at D1 (e.g., *Clidemia* sp. 1 and *Palicourea gibbosa*) produced larger crops here than at the other distances. Recall that TI eliminates the variability associated with crop size because it considers only the number of fruiting individuals. Second, palm fruits made a disproportionate contribution to overall fruit production at D1. Support for this comes from the fact that distance did not have an effect on total number of fruits excluding the Arecaeae (TF-A) (Table 4-2). Third, some species found only at D1 (0-10 m from the forest edge), including *Marcgravia eichleriana*, *Marcgraviastrum subssesilis*, *Miconia pseudoradula*, *M. theaezans*, *Psammisia ferruginea*, *Schefflera lasiogyne*, *Phytolacca rivinoides*, produced large fruit crops. Even though the effect of distance alone was not significant for total number of fruits excluding palms (TF-A), the trend was similar to that for the previous two variables, i.e., sharp decrease from forest edge towards forest interior.

The effect of distance on fruit abundance was modified by edge age and habitat, but neither factor alone had an effect on any of the variables describing fruit abundance (Table 4-2). The interaction between edge age and distance from the forest edge was significant for total number of

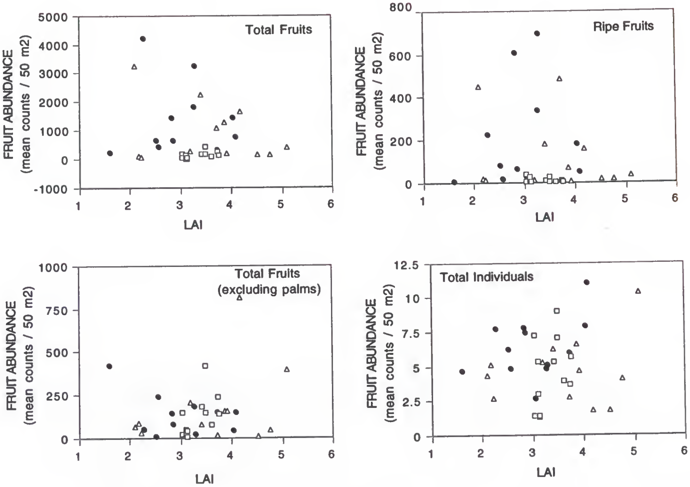


Figure 4-2. Leaf area index (LAI) and mean counts expressing fruit abundance. Symbols represent old edges. Open squares = Pialapi, open tirangles = Célimo II, and filled circles = Célimo I.

fruits (TF) (ANOVA, $F_{3,12} = 2.56$, $P = 0.1$; Table 4-2). Total number of fruits (TF) showed a sharp decline from the forest edge towards the forest interior at new edges and remained almost unchanged at old edges (Fig. 4-4). The interaction between habitat and distance from the forest edge was significant for total number of fruits (TF) (ANOVA, $F_{3,16} = 2.95$, $P = 0.06$) and for total number of ripe fruits (RF) (ANOVA, $F_{3,16} = 3.5$, $P = 0.04$; Table 4-2). For both variables, fruit abundance at D1 (0-10 m from forest edge) was higher in gaps than in forest interior (Fig. 4-5). These differences disappeared at the other distances. The fact that none of these interactions was significant for total number of fruits excluding palms (TF-A), suggests that palms made an important contribution to these results.

The number of ripe fruits (RF) differed significantly between old and new edges depending on month (ANOVA, $F_{10,40} = 2.8$, $P = 0.009$; Table 4-2, Fig. 4-6). The total number of fruiting individuals (TI) and the total number of fruits excluding Arecaceae (TF-A) differed across the four distances in some months but not in others as shown by the significant interaction between distance from edge and month (ANOVA, $F_{30,120} = 1.48$, $P = 0.07$ and $F_{30,120} = 1.57$, $P = 0.04$, respectively; Table 4-2, Fig. 4-7). These results contrast with those for TF and RF, in which this interaction was not significant but in which fruit abundance averaged over time was affected by distance (Table 4-2). Recall that the total number of fruiting individuals (TI) and the total number of

Table 4-2. Results of ANOVAs for Mixed Factorial Designs (Split-split-plot, 1 repeated measure) on mean counts/50 m^2 of number of fruiting individuals (TI), number of fruits (TF), number of ripe fruits (RF), and number of fruits excluding Arecaceae (TF-A). ° log-transformed data. Significance at 10% (*),5% (**), and 1% (***).

Variable	Age (A)			Edge(Age) Error			Distance (D)			Distance x Age			D x E(A) Error	
	df	F		df	SS		df	F		df	F		df	SS
TI	1	0.99		4	1256.13		3	1.77		3	0.65		12	1745.05
TF°	1	0.28		4	71.37		3	4.34	**	3	2.56	*	12	67.2
TF-A°	1	1.26		4	39.18		3	1.43		3	0.4		12	73.79
RF°	1	0.47		4	40.58		3	5.38	**	3	0.96		12	31.67
	Habitat (H)			H x D			H x A			H x D x A			Hx[E(A)xD] Error	
	df	F		df	F		df	F		df	F		df	SS
TI	1	0.74		3	2.24		1	0.522		3	0.016		16	1522.51
TF°	1	0.058		3	2.95	*	1	0.047		3	0.41		16	65.02
TF-A°	1	1.26		3	0.77		1	0.244		3	0.165		16	42.28
RF°	1	0.26		3	3.47	**	1	0.01		3	1.02		16	29.38
	Month x H			M x D x H			M x A x H			M x A x D x H			MxHx[DxE(A)] Error	
	df	F	H-F	df	F		df	F		df	F		df	SS
TI	10	0.86		30	1.27		10	0.31		30	1.28		160	389.1
TF°	10	2.03	**	30	0.55		10	0.37		30	0.6		160	32.45
TF-A°	10	1.42		30	0.58		10	0.69		30	1.28		160	24.58
RF°	10	2.01	**	30	0.41		10	0.94		30	0.62		160	54.78
	M x A			M x E(A) Error			M x D			M x D x A			M x D x E(A) Error	
	df	F	H-F	df	SS		df	F	H-F	df	F		df	SS
TI	10	1.47		40	144.98		30	1.48	*	30	1.09		120	350.03
TF°	10	0.49		40	21.43		30	1.29		30	0.99		120	25.43
TF-A°	10	0.65		40	17.25		30	1.57	**	30	0.7		120	22.13
RF°	10	2.83	***	40	1.27		30	0.76		30	1.17		120	43.2

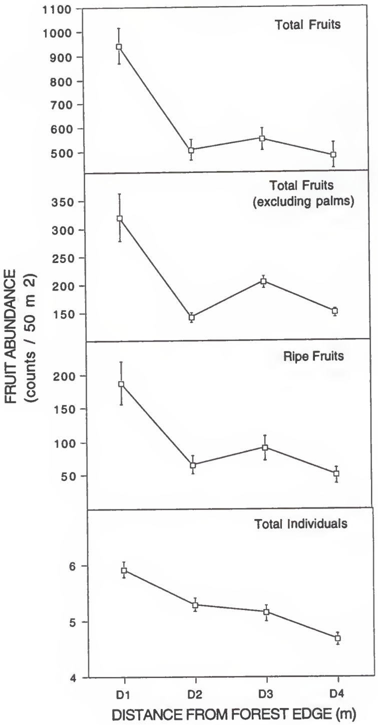


Figure 4-3. Variation in fruit abundance at the Reserva Natural La Planada in relation to distance from forest edge. Points represent means and bars standard errors.

fruits excluding Arecaceae (TF-A) eliminates part of the variability associated with crop size because (1) TI considers only the number of fruiting individuals and (2) TF-A includes plant species producing smaller and less persistent fruit crops, i.e., number of fruits per reproductive season, than those of palms and plant species producing similar number of fruits.

Lastly, fruit abundance expressed as the total number of fruits (TF) and total number of ripe fruits (RF) differed significantly between gaps and interior, but depended on month, as shown by the significant interaction between habitat and month (ANOVA, $F_{10,160} = 2.0$, $P = 0.03$ and $F_{10,160} = 2.0$, $P = 0.03$, respectively; Table 4-2). The Arecaceae again seemed to be mostly responsible for this result as indicated by the fact that this interaction was not significant for the total number of fruits when the Arecaceae were excluded (TF-A) (Table 4-2).

Species Level Responses

I recorded 149 plant species fruiting in the understory of the edges included in this study and classified them in five categories: extremely sparse (1 individual), very sparse (2-5 individuals), sparse (6-20 individuals), abundant (21-50 individuals), and very abundant ($\geq$51 individuals). Of 149 species, 26 (17%) were abundant to very abundant ($\geq$21 individuals) and 125 (83%) were sparse to extremely sparse (<21 individuals) (Appendix A). The most abundant species

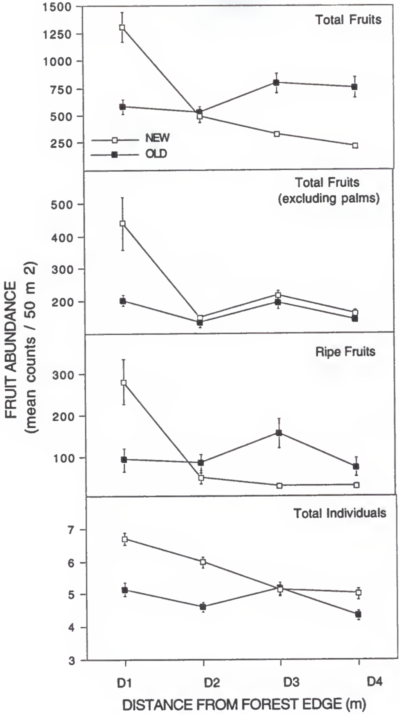


Figure 4-4. Variation in fruit abundance at the Reserva Natural La Planada in relation to edge age and distance from forest edge. Points represent means and bars standard errors.

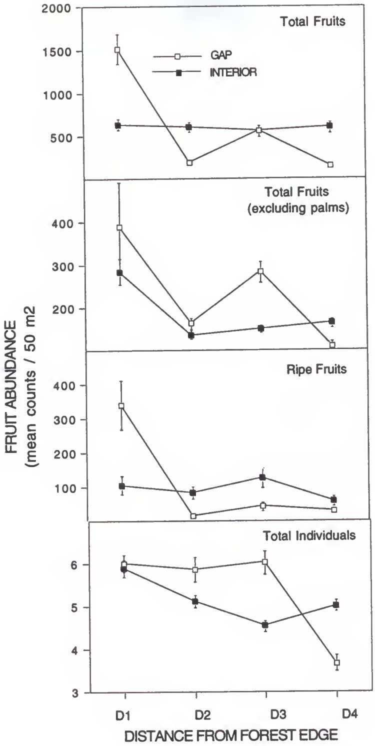


Figure 4-5. Variation in fruit abundance at the Reserva Natural La Planada in relation to habitat and distance from forest edge. Points represent means and bars standard errors.

were two Rubiaceae, Faramea affinis and Palicourea gibbosa. One hundred species were found both at new and old edges and 49 were exclusive to new (35 species) and old edges (14 species) (Appendix A). In this respect, new edges presented proportionally more species than old edges (Goodness of Fit test, $G = 9.3$, $P < 0.01$).

Fruit abundance on a species by species level, expressed as the number of fruiting individuals, varied depending on distance from the edge and edge age. The distribution of fruiting individuals for 16 of the 26 abundant species departed significantly from a uniform distribution across the four distances (Table 4-3). Given a 10% probability of obtaining a species that shows a non-uniform distribution it is very unlikely that 16 or more species out of 26 would have shown a non-uniform distribution by chance alone (Binomial test, $P = 2.0 \times 10^{-10}$). Clearly, the distribution of fruiting individuals of some species is affected by the creation of edges.

For the 16 species showing a non-uniform distribution I used residuals to further determine if they were more abundant at any particular distance from the forest edge (i.e., if at any given distance the observed frequency was greater than the expected frequency). Four species were more abundant at D1 (0-10 m), three species were more abundant at D4 (190-200 m), four species were more abundant at D2 (30-40 m) or D3 (60-70 m), and five species were more abundant at two different distances (e.g., Alloplectus tetragonus and

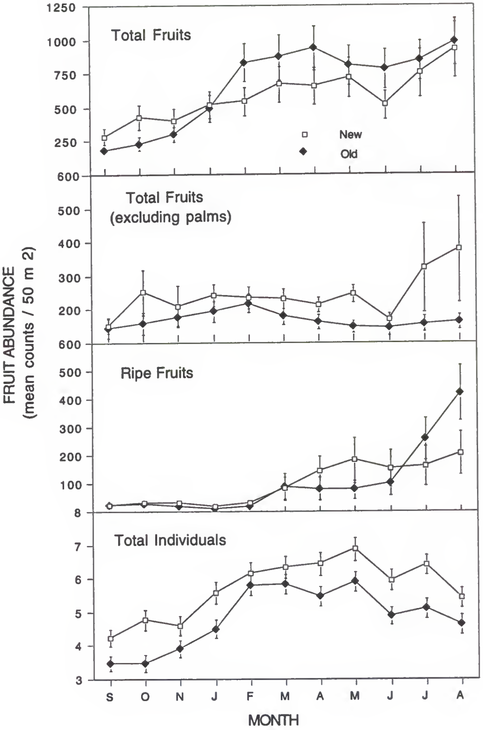


Figure 4-6. Variation in fruit abundance at the Reserva Natural La Planada in relation to edge age and month. Points represent means and bars standard errors.

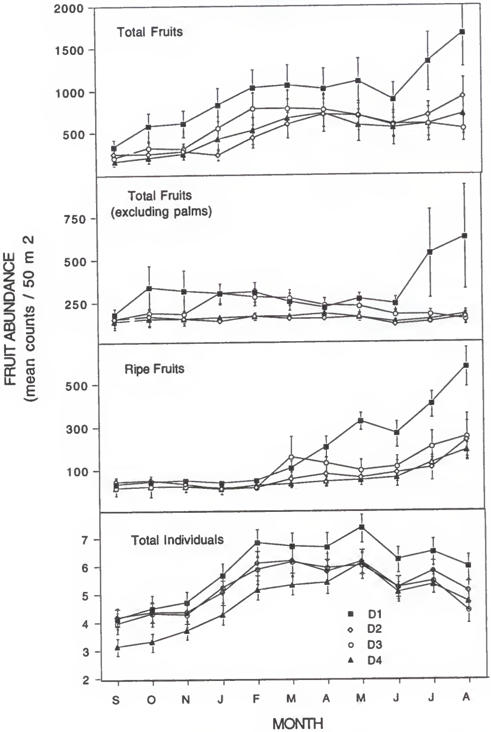


Figure 4-7. Variation in fruit abundance at the Reserva Natural La Planada in relation to distance from forest edge and month. Points represent means and bars standard errors.

Palicourea gibbosa), the latter suggesting a bimodal distribution (Table 4-3). Species showing bimodal distributions, in particular, suggest that distance alone can not explain their distribution across the pasture-forest edge.

I evaluated the combined effect of distance and edge age on the number of fruiting individuals for 16 species (Table 4-4). For nine species there was a significant interaction between distance and edge age, indicating that the distribution of fruiting individuals across the four distances differed between old and new edges ($G_{Heterogeneity}$, $P \leq 0.1$, Table 4-4). A significant interaction between distance and edge age was irrespective of whether the species showed a non-uniform distribution across the four distances by combining the two types of edges (G_{Pooled}, $P \leq 0.1$, Table 4-3) or by looking at old and new edges separately (G_{Old}, $P \leq 0.1$ and G_{New}, $P \leq 0.1$, Table 4-4).

Most of the fruiting individuals found at my study edges were represented by few individuals, precluding the use of Goodness of Fit Test to establish how distance from forest edge affected their distribution. Instead, I used information on their abundance (Table 4-5) to establish the distance at which sparse species were found more often. I excluded abundant and very abundant species from the analysis and found that for the remaining three groups of plants abundance and distance from the edge were not independent (Test for Independence, $\chi^2 = 18.86$, $P = 0.004$). Examination

Table 4-3. Distribution of fruiting individuals of abundant (≥21 individuals) plant species in the understory of La Planada in relation to distance from the edge. Numbers represent number of individuals. Distances are 0-10 m (D1), 30-40 m (D2), 60-70 m (D3), and 190-200 m (D4) from forest edge. $P < 0.1$ (*), $P < 0.05$ (**), $P < 0.01$ (***), $P < 0.001$ (****).

Species	D1	D2	D3	D4	G-stat
Uniform Distribution					
Burmeistera carnosa	10	11	13	14	0.83^{ns}
Solanum sp.7	14	15	11	11	0.99^{ns}
Anthurium membranaceum	32	30	27	24	1.31^{ns}
Burmeistera sp. nov.	7	4	5	9	2.35^{ns}
Anthurium umbraculum	17	17	13	23	2.87^{ns}
Columnea cinerea	10	5	4	5	3.34^{ns}
Spheraedenia steyermarkii	7	2	6	6	3.37^{ns}
Anthurium cf. *pulverulentum*	8	6	5	2	3.99^{ns}
Anthurium versicolor	18	8	16	14	4.36^{ns}
Geonoma weberbaueri	19	20	9	14	5.29^{ns}
Non-Uniform Distribution					
Psammisia aff. *debilis*	20	9	4	8	12.9 ***
Besleria solanoides	39	16	14	4	35.5 ****
Psycothria aubletiana	45	14	12	5	40.3 ****
Clidemia sp.1	54	59	27	10	48.7 ****
Solanum sp.5	3	14	14	17	12.2 ***
Chamaedorea polychlada	5	7	15	18	10.8 **
Alloplectus tenuis	2	2	7	9	8.0 **
Asplundia sp.1	2	10	5	8	6.6 *
Anthurium umbricolum	9	7	22	7	12.2 ***
Anthurium cf. *marmoratum*	10	9	17	5	7.2 *
Faramea affinis	104	146	127	117	7.6 *
Alloplectus teuscheri	22	41	18	30	10.9 ***
Anthurium carchiense	3	15	5	12	11.7 ***
Anthurium cf. *melampyi*	20	10	19	32	12.3 ***
Palicourea gibbosa	91	65	91	43	23.6 ****
Alloplectus tetragonus	10	2	7	1	11.7 ***

Table 4-4. Results of Replicated Goodness of Fit Test on the number of individuals in fruit for understory plants at the Reserva Natural La Planada. $G_{Heterogeneity}$ (G_H) , G_{Total} (G_T), G_{Old} edges (G_O), and G_{New} edges (G_N). $P < 0.1$ (*), $P < 0.05$ (**), $P < 0.01$ (***), $P < 0.001$ (****).

Species	df	G_H	df	G_T	df	G_O	df	G_N
Anthurium versicolor	3	6.64 *	6	11 *	3	1.48 ns	3	9.49 **
Anthurium cf. *marmoratum*	3	7.88 **	6	15.08 **	3	10.72 **	3	4.3 ns
Anthurium umbricolum	3	28.28 ****	6	40.48 ****	3	17.96 ****	3	3.22 ns
Alloplectus teuscheri	3	7.72 *	6	18.6 ***	3	5.06 ns	3	13.52 ***
Geonoma weberbaueri	3	17.56 ****	6	22.86 ****	3	3.93 ns	3	18.92 ****
Solanum sp.7	3	6.84 *	6	7.83 **	3	2.65 ns	3	5.18 ns
Anthurium cf. *melampyi*	3	21.76 ****	6	34.02 ****	3	17.38 ****	3	16.6 ****
Palicourea gibbosa	3	6.32 *	6	29.93 ****	3	16.77 ****	3	13.14 ***
Solanum sp.5	3	6.24 *		18.38 ****		7.16 *		11.19 **
Anthurium membranaceum	3	0.94 ns	6	0.94 ns	3	1.74 ns	3	0.49 ns
Burmesitera carnosa	3	3.47 ns	6	4.32 ns	3	2.39 ns	3	1.89 ns
Clidemia sp.1	3	2.42 ns	6	51.11 ****	3	32.79 ****	3	18.12 ****
Psycothria aubletiana	3	3.84 ns	6	44.15 ****	3	24.29 ****	3	19.83 ****
Faramea elegans	3	2.24 ns	6	2.25 ns	3	3.35 ns	3	6.48 *
Besleria solanoides	3	4.04 ns	6	39.5 ****	3	35.13 ****	3	4.35 ns
Chamaedorea polychlada	3	3.32 ns	6	14.14 **	3	12.45 ***	3	1.69 ns

Table 4-5. Distribution of fruiting individuals in the understory of the Reserva Natural La Planada across pasture-forest edge based on species abundance. Numbers represent the number of fruiting individuals.

	Number of	Distance			
	Species	D1	D2	D3	D4
Extremely sparse (1 individual)	33	13	4	7	9
Very sparse (2-5 individuals)	40	64	21	28	25
Sparse (6-20 individuals)	50	167	144	138	120
Abundant (21-50 individuals)	13	94	99	115	137
Very abundant (≥51 individuals)	12	475	441	384	327

of the residuals showed that more individuals of very sparse species were found at D1 and of sparse species at D2. Although individuals of both groups of plants might be found across the four distances, these results show that sparse species are found more often close to the edges.

Seed movement

I recovered 393 bird droppings from 19 species of mist-netted frugivorous birds. Seeds of 93 species, of which I was able to identify 65, were represented. Of the species I identified, 52 (80%) were found in the subquadrats where I counted fruits. This figure, compared to the total number of plant species I recorded fruiting in the understory (149), shows that bird droppings represent a subsample of the plant species that I found.

The number of plant species in individual bird droppings ranged from 1 to 7 (mean ± SD, 1.7 ± 1.0, N = 393). There was no significant difference in the mean number of plant species in droppings recovered at the four distances (ANOVA, $F_{3,393} = 0.8$, $P = 0.5$). In addition, total numbers of seeds in bird droppings was independent of distance (χ^2 Test for Independence, df = 15, $\chi^2 = 12.8$, $P = 0.6$) .

Fourteen of the 26 abundant species ($\geq$21 individuals) and 38 of the 124 sparse species (<21 individuals) fruiting in the understory were represented in the bird droppings (Appendix A). Since sparse species were found more often at the forest edge, I compared their distribution against that of droppings containing their seeds to determine whether they were independent of each other. Plants and droppings were classified as (1) "edge" if the number of observations at D1 (0-10 m) and D2 (30-40 m) combined together was >0, (2) "interior" if the number of observations at D3 (60-70 m) and D4 (190-200 m) was >0, and (3) "edge=interior" if the number of observations at D1 and D2 = D3 and D4. I found that the proportion of droppings containing seeds of sparse species was independent of their abundance in edge and interior (Test for Independence, $\chi^2 = 2.4$, df= 4, $P = 0.6$). Even though sparse species were found more often at forest edge, their seeds are potentially reaching forest interior.

Discussion

Distance from the edge towards the forest interior had a major effect on fruit abundance but only close to the forest edge. Nevertheless, the facts that (1) the effect of distance was modified by edge age, habitat, and month of the year, and (2) results for the four variables describing fruit abundance differed, indicate that there are complex interactions between edges and fruiting plants (summarized in Table 4-6). I interpret these complex interactions in terms of scales at which fruit abundance changes in relation to the creation of edges.

At the scale defined by the pastures and the forest matrix and by the length of the study (1 yr), new edges generated spatial heterogeneity in fruit abundance within the study area at D1 (0-10 m from forest edge). Fruit abundance, expressed as total number of fruits (TF) and as total number of ripe fruits (RF), was higher in new than in old edges at D1 but these differences were not evident at the other distances. At the scale defined by the edges and by the length of this study, treefall gaps at D1 generated spatial heterogeneity in fruit abundance within edges. Fruit abundance, expressed as total number of fruits (TF) and as total number of ripe fruits (RF) was higher in treefall gaps than in forest interior at D1 but, again, these differences were not found at the other distances.

When I looked at total number of ripe fruits (RF), and in addition examined the total number of fruits excluding the Arecaceae (TF-A) and the number of fruiting individuals (TI), a different picture emerged. At the scale of the study area and month, RF differed between old and new edges but depended on month. At the scale of edges and month, TF-A and TI differed among the four distances but also depended on month.

These results suggest that changes in fruit abundance and the magnitude of these changes across pasture-forest edge are related to the size of fruit "patches". In my study area, large patches of fruit were generated by understory palms, which produced large fruit crops that persisted for a long time. These large fruit patches seemed to generate a steep gradient in fruit abundance from the edge towards the forest interior on a yearly basis. Conversely, small patches of fruit seemed to generate gradients that varied in their magnitude depending on month. I will discuss these results

Table 4-6. Summary of results of ANOVAs on fruit abundance across the pasture-forest edge for the different response variables. Fruit abundance expressed as total number of fruits (TF), total number of ripe fruits (RF), total number of fruits excluding the Arecaceae (TF-A), and total number of fruiting individuals (TI). Significance at 10% (*), 5% (**), 1% (***).

	TF	RF	TF-A	TI
	Large Fruit Crops		Small Fruit Crops	
ANOVA terms				
Distance	**	**		
Distance x Age	*			
Distance x Habitat	*	**		
Distance x Month			**	*
Age x Month		***		
Habitat x Month	**	**		

in terms of (1) the factors that influence fruit abundance and (2) the consequences that these observed changes might have on plants and frugivores.

Factors Influencing Fruit Abundance

Fruit abundance is regulated by abiotic and biotic factors interacting in complex ways with the flowering and/or fruiting stages of a plant's life cycle (e.g., Marshall and Grace 1992). Abiotic factors that have a direct effect on fruit numbers and fruit size are photoperiod and irradiance (e.g., Auchter et al. 1926; May and Antcliff 1963; Jackson and Palmer 1977; Mathai and Sastry 1988; Tombesi et al. 1994), temperature (e.g., Chaikiattiyos et al. 1994), water availability (e.g., George et al. 1990), and nutrients (e.g., Stephenson 1992). Biotic factors include pollination, predation of flowers, seeds, and fruits, and damage by pathogens (Stephenson 1981). The importance of these factors is likely to differ within and among species, depending on habitat.

Irradiance is an important factor influencing fruit abundance. Most work that supports this contention is based on the observation that when irradiance increases in a forest as a result of disturbance, so does fruit abundance (Halls 1973; Piñero and Sarukhan 1982; Clark and Clark 1987; Ågren 1988; Levey 1990). Although I did not measure irradiance directly, my estimates of leaf area index (LAI) describe indirectly the light environment at my edges. I found that

(1) LAI did not correlate with fruit abundance at old edges, (2) LAI did not change significantly with distance from forest edge, (3) treefall gaps alone did not influence fruit abundance (but see the significant interaction between habitat and distance, and between habitat and month, on TF and RF), and (4) distance from edge influenced fruit abundance in complex ways. Thus, irradiance alone cannot explain my findings. Other abiotic factors, such as temperature, water availability, and nutrients, likely influence fruit abundance across the pasture-forest edge.

In tropical areas flower and fruit abundance are influenced by low temperatures (Tutin and Fernandez 1993), soil fertility (Gentry and Emmons 1987), water availability (Heideman 1989; Seghieri et al. 1995), and pollination (Compton et al. 1994). During the dry season (June-August), La Planada experiences clear skies, low rainfall, strong winds, and extreme maximum and minimum temperatures. The effect of these factors on understory vegetation may be exacerbated at the pasture-forest edge, thereby influencing changes in fruit abundance. For instance, during this period, leaves of understory plants and vines at the forest edge but not in the interior wilted and abscised. At a montane locality north of La Planada, soil moisture across the pasture-forest edge changed progressively over the dry season and reached its lowest value 10 m from the forest edge towards forest interior (Murcia 1993). At a lowland tropical site, vapor pressure deficit (VPD) in the understory changed across the pasture-forest edge, decreasing towards the forest interior (Kapos 1989; Seizer 1992). More important, however, were the differences found between the wet and dry season, higher VPD values being recorded farther inside the forest during the dry than during the wet season (Seizer 1992). At the same lowland site, Kapos et al. (1993) compared the carbon isotopic composition (∂^{13}C) of leaves of two canopy and two understory species and found that the ∂^{13}C concentration decreased from the edge towards the forest interior for the understory but not for the canopy species. These changes were more pronounced for *Duguetia* aff. *flagellaris* (Annonaceae) than for *Astrocaryium sociale* (Arecaceae). The results described by Kapos et al. (1993) indicate that the understory environment might be more sensitive to edge creation than the canopy and that understory species vary in their sensitivity to the factors that influence their distribution.

At La Planada, increases in fruit abundance at the forest edge could also be related to changes in soil fertility as a result of increased litterfall during the dry season, and deposition of volcanic ash at edges. La Planada is influenced by several active volcanoes that release andesitic ash (Mizota and van Reenwyk 1989, cited in van Wambeke 1992) rich in nutrients (Shoji et al. 1993). These air-borne particles might be deposited disproportionately along pasture-forest edges. Some studies have shown that edges alter the deposition of dry airborne material such that deposition rates decrease from the forest edge towards the forest interior (Geiger 1965; Draiijers et al. 1988). In an area like La Planada, which is characterized by nutrient-poor soils, the addition of nutrients could affect the production of fruits.

A combination of several factors then may account for the changes I observed in fruit abundance for individual species and for the entire understory plant assemblage. I propose that changes in TF-A and TI across the four distances depending on month, are the result of within-year variability in environmental conditions. On the other hand, changes in TF and RF over the year may be the result of increased irradiance at the forest edge due to direct exposure of the pasture-forest interface to sunlight. Recall that TF and RF, which included counts of palm fruits, were most influenced by distance from forest edge. This is consistent with Blanchard's (1992) results showing that increased abundance of palm fruits at the forest edge is correlated with increased light levels.

Consequences for Plants and Frugivores

Studies looking at the effect of edges on plants have focused more on the vegetative (e.g., Ranney et al. 1981; Chen et al. 1992; Seizer 1992; Young 1993; Matlack 1993) than on the reproductive stage (Romano 1990; Willimas-Linera 1990; Blanchard 1992; Murcia 1993) of their life cycle. The former provides information on the structure and productivity of the edge. The latter provides information on the persistence of edges through time, depending on the ability of plants to complete their life cycle, including the production and dispersal of seeds, in a given environment.

Increases in fruit abundance, and thus of seed outputs, can have different consequences for individuals, populations, and assemblages. A numerical increase in fruit production by an individual can affect traits, such as seed size (Ågren 1988, 1989), and thus seedling performance (Westoby et al. 1992). Changes in fruit numbers at the population level can affect recruitment rates (e.g., Kellman and Kading 1992, Guimarães et al. 1994). For plant assemblages, an increase in fruit numbers can affect colonization rates of disturbed areas and thus alter species composition. In all cases, changes in fruit numbers can affect the behavior of dispersers (Murray 1987; Loiselle and Blake 1993).

At La Planada, the distribution of fruiting individuals was influenced by the presence of edges. Changes in the number of fruiting individuals at any given distance from the forest edge may indicate differences in recruitment rates at different distances. Plant establishment, growth, reproduction, and seed dispersal are very likely to be influenced by distance from forest edge in various ways resulting in the observed distributions of fruiting individuals (Chapter 3). It is possible that if edge conditions remain unaltered over time, i.e., pastures and fields are maintained as such, the observed distributions will persist and even become more pronounced.

Sparse species constituted an important component of the assemblage of understory plants of La Planada. Little is known about habitat preferences of these species, but clearly they represent species typical of large disturbed areas, forest gaps, and forest (Appendix A). Sparse species were most abundant close to the pasture-forest interface (D1 and D2) within edges and at new edges within the study area (34 species were found exclusively at new edges compared with 14 at old edges) (Appendix A). In addition, for the few sparse species from which I recovered seeds in bird droppings, I found that the proportion of fruiting individuals at the "edge" and "interior" was independent of the proportion of bird droppings that contained their seeds and were recovered in these two zones. Thus, forest edges are being colonized by sparse species and factors other than seed dispersal might be influencing recruitment rates across the pasture-forest edge.

Changes in fruit abundance across the pasture-forest edge partially paralleled that of bird captures (Chapter 5). Increased fruit abundance, expressed as total fruits (TF) and total ripe fruits (RF), was mirrored by an increase in frugivore capture rates only at D1 (Chapter 5). The opposite was true at D4 where fruit abundance reached the lowest values but frugivore capture rates were the highest (Chapter 5). The high fruit production at D1 was mainly due to palms.

Bird species known to feed on palm fruits at La Planada, including Myadestes ralloides, Lipaugus cryptolophus, Semnornis ramphastinus, Pipreola riefferi, Entamodestes coracinnus (C. Restrepo personal observation, Restrepo 1990) and Andigena laminirostris (Beltran 1991) did not account for the high capture rates observed at D1. Thus it is unclear whether changes in TF and RF across the pasture-forest edge influenced the behavior of frugivorous birds. The contrary might be true, however, for TF-A and TI. Those species known to feed on fruits other than palms, which were the majority of frugivorous species captured with mist nets, made an important contribution to the high capture rates observed at D1. Moreover, as occurred with TF-A and TI, there was a significant interaction between distance from edge and month on capture rates of frugivores (Chapter 5).

This study showed that edges influenced fruit abundance in different ways. First, fruit production by the assemblage of understory plants changed abruptly from forest edge towards forest interior but depended on edge age, the presence of treefall gaps, the length of the observations, and whether or not palms were taken into accout. Second, fruit production on a species by species level, and expressed as the total number of fruiting individuals, changed across the pasture-forest edge. This was shown both among abundant and sparse species. The latter provided evidence to support the contention that edges represent zones of opportunities for the establishment of a wide range of species.

CHAPTER 5
EDGES AND UNDERSTORY BIRDS IN A NEOTROPICAL MONTANE FOREST

Introduction

Natural disturbances play a major role in maintaining high levels of diversity in tropical ecosystems (e.g., Connell 1978, Salo et al. 1986, Bush 1994, Gentry 1986; but see Haffer 1969, Hubbell and Foster 1987). At regional scales, one result of disturbance is the creation of ecotones, which have been postulated to favor speciation processes (Bush 1994) and high species richness (Terborgh 1977, Bush 1994). Human disturbances, on the other hand, have resulted in a variety of land uses. Focus has now shifted towards understanding how human disturbances affect distributions of species (e.g., Kattan 1992) and how this might impact ecosystem processes (Vitousek 1990, Kruess and Tschnarntke 1994, Tilman and Downing 1994).

One consequence of human activities on landscapes is the creation of sharp edges bounding disturbed areas, such as pastures, logged forest stands, and agricultural fields. These edges, whether found in little or highly modified landscapes, may influence the movement of organisms between the undisturbed and disturbed areas (Wiens et al. 1985, Wiens 1992). It is very likely that edges, by influencing the movement of animals, might indirectly affect ecological processes mediated through plant-animal interactions such as pollination and seed dispersal. In tropical systems many organisms are involved in plant-animal interactions. For the most part, work done in the tropics has focused on how edges affect animal distributions (Quintela 1986, Laurance 1990, Malcolm 1994). Less emphasis has been given to how edges influence the distribution of animals mediating ecological processes.

The extent to which edges can affect the distribution of organisms varies with edge age (e.g., Williams-Linera 1990), and land use (e.g., DeGraaf 1992) may determine the degree to which edges can affect organisms. Equally important is the variation among organisms in their response to edges (e.g., Kroodsma 1984, Noss 1991). Such variation can be used to tease apart the mechanisms underlying such responses. Possible mechanisms include changes in the resource base (Malcolm 1991), parasites and predators (e.g., Gates and Gysel 1978, Brittingham and Temple 1983, Loye and Carroll 1995), physiological condition of organisms (Wiens et al. 1985), dispersal, and home range size (Kuitunen and Mäkim 1993).

Here I report on how edges influence the distribution of understory birds in a neotropical montane forest. I looked at the effects of distance from the edge towards the forest interior and time since edge creation on birds classified by feeding guilds. I concentrated on frugivores and nectarivores, since a high proportion of understory plants in neotropical cloud forests rely on these two groups of organisms for seed dispersal and pollination (Terborgh 1977, Gentry 1983, Stiles 1985). Thus, changes in their distribution may help explain how edges influence seed dispersal and pollination in highly fragmented habitats.

Methods

Understory Birds

I mist netted birds at six edges, three old and three new, each netting site encompassing an area 100 x 200 m (2 ha) (Chapter 2). Strips at four distances from the forest edge towards the forest interior (D1: 0-10, D2: 30-40, D3: 60-70, and D4: 190-200 m) were divided into 5 plots (20 x 10 m) (Chapter 2) (Fig. 2-3). Three of these plots were chosen at random and one pair of mist nets was placed in each, with one net set perpendicular to the other. Nets were 9 X 2.5 m with a 32 mesh. In each strip, nets were separated by a mean distance of 40 m and positioned 0.5 m above the ground.

I operated 12 pairs of mist nets simultaneously from 0530-1300 for two consecutive days per month per distance per edge, trying to complete when possible 14 hours of mist netting per pair of mist nets. Mist netting started in June 1992 at the old edges. In September 1992 I included the new edges. Thus the six edges were sampled simultaneously from September 1992-August 1993, excluding December 1992 when I did not sample birds. Because the sampling unit was a pair of mist nets, instead of the traditional single net, I define mist net hours as the hours that a pair of nets was opened. In total the mist netting effort was equivalent to 11,892 net-hours. Mist nets were checked every 1-1.5 hours, and for each captured bird I recorded species, mist net number, molt, presence of cloacal protuberance or brood patch, fat, mass, culmen length (total and exposed), culmen height and width, tarsus and tail length, and wing chord. All birds, except hummingbirds, were individually marked with color bands. Hummingbirds were marked temporarily by clipping the tip of their tail and wing feathers to recognize recaptures within a mist netting session. Bird abundance is expressed throughout this paper as capture rates, i.e., number of captures per pair of mist nets per 100 mist net hours (mnh). Recaptures on the same day were excluded from the analyses.

Birds were classified into four feeding guilds: frugivores, insectivores, nectarivores, and carnivores. Frugivores were defined as species that commonly consumed fruit and/or seeds; most of them also consumed insects to some degree. Insectivores ate primarily insects. Nectarivores relied heavily on nectar and included nectar "thieves." Carnivores primarily preyed on vertebrates. The placement of any given species in one of these categories was based on the analysis of fecal samples, my own observations, and published reports (Miller 1963, Stiles and Skutch 1989, Andrade et al. 1993, Arango 1993).

The use of mist nets versus acoustic and/or visual censuses to carry out studies on bird assemblages in the tropics has been widely discussed because of the biases inherent in any sampling method (e.g., Terborgh and Weske 1969, Terborgh 1971, Karr 1971, Remsen and Parker 1983, Karr 1981a,b, Lynch 1989, Remsen 1994). It is accepted that mist nets only sample a proportion of bird species found in an area (Terborgh and Weske 1969, Karr 1981b); that if used over a prolonged period birds learn the position of nets (Terborgh 1977, Bierregaard 1990); and that figures on bird abundance might overestimate the abundance of many species (Karr 1981b, Remsen and Parker 1983, Lynch 1989). In addition, when used to compare habitats that differ markedly in structure, capture rates can be misleading in regard to the presence and abundance of many species (Terborgh 1971, Lynch 1989, Blake et al. 1990). My study, then, only reflects what happens to those birds that are effectively sampled by mist nets in the understory (see also Wong 1986, Levey 1988a,b, Blake and Loiselle 1991, Loiselle and Blake 1991, Poulin et al. 1992). I stress that mist netting took place only inside the forest, and the aim of this study was to compare changes in bird abundance from the edge towards the forest interior. Thus, problems associated with habitat biases are either minimized or held constant.

One possible problem for interpreting the results, however, relates to the timing of mist netting in old and new edges. In old edges mist netting began in June 1992 and in new edges in September 1992. Higher capture rates in new than old edges in September and October could be attributed to birds having learned the position of nets in the old edges. If this increase in capture rates in new edges was a consequence of a learning process then I would expect (1) a decrease in the proportion of recaptures over time for old and new edges, and (2) a higher proportion of recaptures in new than old edges during these months. The data for all species (excluding hummingbirds), frugivores, and insectivores, do not support these predictions. I conclude that any observable difference can therefore be attributed to differences between the two types of edges.

Data Analysis

To establish changes in the abundance of the understory avifauna of La Planada as a function of distance from the edge and edge age I analyzed capture rates for all bird species combined and for three feeding guilds. Carnivores were excluded from the analyses because of small sample size. I used ANOVAs for Mixed Factorial Designs (Girden 1992). Edge age (old and new) was included as a between-subject factor. Month (September 1992-August 1993) and distance (D1-D4) were included as within-subject factors or repeated measures. Month and distance were included as within-factors because of restrictions in the randomization procedure when "assigning" month and distance levels to each edge, which can lead to correlations between the observations (Girden 1992, Manly 1992). Edges were treated as subjects because each edge was measured repeatedly for each of the different treatment combinations. Because mist nets are nested within distance and capture rates were zero for many pairs of mist nets at a given month/distance/edge, I averaged capture rates for each three pairs of mist nets/month/distance/edge. This procedure reduced the dimensionality of the data and also made the data more normally distributed by eliminating many zero values. I plotted the residuals as a function of fitted Y values to detect any violation of assumptions (Manly 1992). The data for all four ANOVAs presented in this paper were square-root-transformed. In addition, I verified the assumption of compound symmetry (i.e., the covariation between each pair of treatments is equal for all subjects) for ANOVAs that included within-factors (Girden 1992, Manly 1992). When compound symmetry is violated, the probability of committing a Type I error increases. To account for this, the degrees of freedom have to be corrected by a factor, epsilon, which ranges from 1/(J-1) to 1.0, where J is the number of levels in a treatment. The closer epsilon is to 1.0, the lower is the probability that compound symmetry is being violated (Girden 1992). Epsilon is estimated based on the conservative Geisser-Greenhouse method and the more liberal Huynh-Feldt method (Girden 1992). In this paper I report the corrected F values based on the liberal Huynh-Feldt method (H-F).

In addition to the above omnibus ANOVA tests, I specified contrasts of mean differences to test specific hypotheses. These hypotheses included effects involving single factors and interactions (Gagnon et al. 1989, Girden 1992). For the distance effect I specified two contrasts, by comparing mean capture rates at D1 and D4 separately with those of D2 and D3 together. I assumed that changes in bird distribution, if any, would be more marked at the extremes. For the distance x age interaction I specified a single contrast, by comparing mean capture rates at D4 between old and new edges. For the month x age and the month x distance interactions I specified two contrasts for each, comparing dry with wet months. I reasoned that because of marked differences in the rainfall regime at La Planada, changes in bird abundance between habitats (distance or type of edge) were more likely to occur between dry and wet months. Dry months were those exhibiting the lowest rainfall records (February and July) and the previous month when rainfall started to decrease (January and June). Wet months were those that received the highest rainfall (April and October) and the previous month when rainfall started to increase (March and September) (Fig. 2-2). For the interaction between month and age I compared the mean number of captures between old and new edges during the dry and wet months. For the interaction month x distance I compared the mean number of captures between D1 and D4 during the dry and wet months. I report the corrected F-values and associated probability in the results section. All analyses were performed using

SuperANOVA (Gagnon et al. 1989).

To determine if individual species were affected by the presence of edges, I performed two related tests based on data collected between June 1992 and August 1993. First, I used a Goodness of Fit test (G-statistic) to determine if the number of captures across the four distances departed significantly from a uniform distribution. Second, I used a Replicated Test of Goodness of Fit (G-statistic) (Sokal and Rohlf 1981) to establish, in addition to the distance effect, an edge age effect on the number of captures. For both tests, monthly captures for each species were pooled, keeping separate the information on old and young edges. For these analyses I chose those species in which at least 80 percent of the expected cell frequencies were greater than 5, since the statistic G departs from the χ^2 distribution if this is not the case (Siegel and Castellan 1988). Five species (_Lipaugus_ _cryptolophus_, _Ocreatus_ _underwoodii_, _Tangara_ _arthus_, _T_. _labradorides_, and _T_. _nigroviridis_) did not meet this criterion but were included in the analyses. The first two were included because of the clear trends they exhibited. The last three species were lumped in the _Tangara_ spp. for the analyses because of similarities in many features of their life history (Isler and Isler 1987).

A vast majority of the species did not meet the above criterion. To evaluate the influence of edges on these species I classified birds into five categories according to capture frequency: extremely sparse (1 capture), very sparse

(2-5 captures), sparse (6-20 captures), abundant (21-50 captures), and very abundant ($\geq$ 51 captures). I assigned capture numbers for each category to the four distances. I used a Chi-square test to evaluate the association between bird abundance and distance and used the residual values to determine the contribution of each cell to the overall result (Siegel and Castellan 1988).

I used an alpha of 10%. The sampling procedure used in my study resulted in an increase of Type II errors and low power of my tests (see Chapter 4). Increasing alpha counterbalances these effects at the cost of increasing Type I errors (Zolman 1993).

Results

Understory Birds

From September 1992 through August 1993 I accumulated 1,789 captures of 80 species. Bird captures differed significantly among the four distances, suggesting that the abundance of understory birds at La Planada is affected by the presence of edges (ANOVA, $F_{4,16} = 7.6$, $P = 0.004$; Table 5-1, Fig. 5-1). Mean capture rates were significantly higher at D1 (mean = 16.9) and D4 (mean = 19.3) than at D2 and D3 combined together (mean = 12.1) (Contrast of Mean Differences, $F_{1,12} = 10.7$, $P = 0.007$ and $F_{1,12} = 18.4$, $P = 0.001$, respectively). Edge age, however, modified the distance effect as shown by the significant distance x edge

Table 5-1. Results of ANOVAs for Mixed Factorial Designs (1 between-, 2 within-factors) on mean capture rates x 100 mist netting hours (mnh) of all birds, frugivores, insectivores, and nectarivores. The month and month x distance x age effects were excluded from this table. (°) based on square root-transformed data. Significance at 10% (*), 5% (**), 1% (***).

	Age (A)			Error Edge (Age)		Distance			Distance x Age			Error D x E(A)	
	df	F		df	SS	df	F	H-F	df	F	H-F	df	SS
All Birds °	1	2.89	ns	4	11.39	3	7.63	***	3	3.54	**	12	22.39
Frugivores °	1	1.77	ns	4	14.27	3	4.85	**	3	2.75	*	12	25.03
Insectivores °	1	0.24	ns	4	18.42	3	2.79	*	3	1.32	ns	12	27.86
Nectarivores	1	0.05	ns	4	17.78	3	1.78	ns	3	1.83	ns	12	24.67

	Month x Age			Error M x E(A)		Month x Distance			Error D x M x E(A)	
	df	F	H-F	df	SS	df	F	H-F	df	SS
All Birds °	10	1.78	*	40	30.07	30	1.10	ns	120	85.84
Frugivores °	10	0.79	ns	40	33.99	30	1.93	***	120	106.78
Insectivores °	10	3.23	***	40	39.91	30	0.78	ns	120	114.94
Nectarivores	10	0.52	ns	40	41.85	30	0.82	ns	120	147.25

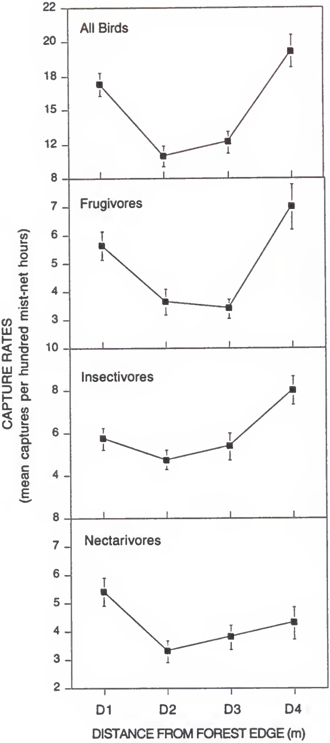


Figure 5-1. Variation in the distribution of understory birds at La Planada in relation to distance from the forest edge. Points represent means and bars standard errors.

interaction (ANOVA, $F_{4,16} = 3.5$, $P = 0.05$; Table 5-1, Fig. 5-2). Capture rates remained very similar at D1, D2, and D3 for old and new edges but differed at D4, where they were higher at new edges (mean = 24.2) than at old edges (mean = 14.1) (Contrast of Mean Differences, $F_{1,12} = 12.0$, $P = 0.005$).

The effect of month on capture rates for all birds was significant (ANOVA, $F_{15,59} = 2.9$, $P = 0.008$). However, changes in bird captures over the year depended on edge age as shown by the significant edge age x month interaction (ANOVA, $F = {}_{15,59} = 2.1$, $P = 0.09$; Table 5-1, Fig. 5-3). This suggests that edge features, such as edge age, can influence the distribution of birds, depending on season. Old and new edges did not differ significantly in regard to bird captures during the dry months (Contrast of Mean Differences, $F_{1,40} = 1.5$, $P = 0.2$) but they did differ during the wet months (Contrast of Mean Differences, $F_{1,40} = 13.1$, $P = 0.0008$).

Feeding Guild Responses to Edges

The abundance of frugivores and insectivores differed significantly with distance (ANOVA, $F_{3,12} = 4.9$, $P = 0.02$ and $F_{3,12} = 2.1$, $P = 0.08$, respectively, Table 5-1, Fig. 5-1). Capture rates for frugivores were significantly higher at D1 (mean = 5.6) and D4 (mean = 7.0) compared to D2 and D3 combined (mean = 3.5) (Contrast of Mean Differences, $F_{1,12} = 7.0$, $P = 0.02$ and $F_{1,12} = 12.0$, $P = 0.005$,

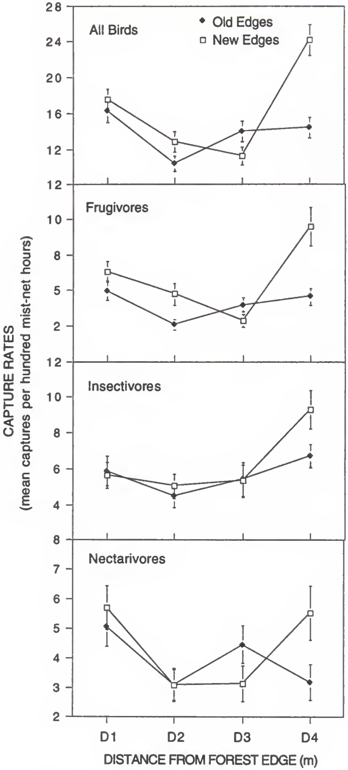


Figure 5-2. Variation in the distribution of understory birds at La Planada in relation to edge age and distance from the forest edge. Points represent means and bars standard errors.

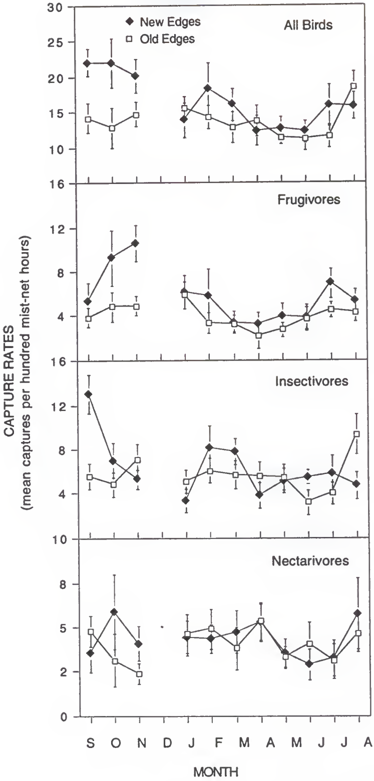


Figure 5-3. Variation in the distribution of understory birds at La Planada in relation to edge age and month. Points represent means and bars standard errors.

respectively). Capture rates per 100 mist-net hours for insectivores were significantly higher at D4 (mean = 8.0) compared to D2 and D3 combined together (mean = 5.0) (Contrast of Mean Differences, $F_{1,12} = 8.3$, $P = 0.01$) but did not differ between D1 and D2-D3 combined. The omnibus test showed that distance from the forest edge did not affect nectarivore capture rates (Table 5-1, Fig. 5-1). Nevertheless, the specific hypothesis tested by contrast of mean differences showed that nectarivores were more abundant at D1 (mean = 5.4) than at D2 and D3 combined (mean = 3.5) (Contrast of Mean Differences, $F_{1,12} = 4.9$, $P = 0.05$).

Among frugivores, the distance effect was modified by edge age, as shown by the significant interaction between these two factors (ANOVA, $F_{3,12} = 2.7$, $P = 0.09$; Table 5-1, Fig. 5-2). Capture rates at D1, D2, and D3 were similar between old and new edges. However, capture rates at D4 were significantly higher at new (mean = 9.4) than at old (mean = 4.5) edges (Contrasts of Mean Differences, $F_{1,12} = 7.2$, $P = 0.02$). The interaction between distance from the edge and edge age in the omnibus test was not significant for insectivores and nectarivores (Table 5-1, Fig. 5-2). Nevertheless, when testing specific hypotheses I found that capture rates for nectarivores at D4 were significantly higher at new (mean = 5.5) than at old (mean = 3.3) edges (Contrast of Mean Differences, $F_{1,12} = 4.0$, $P = 0.07$).

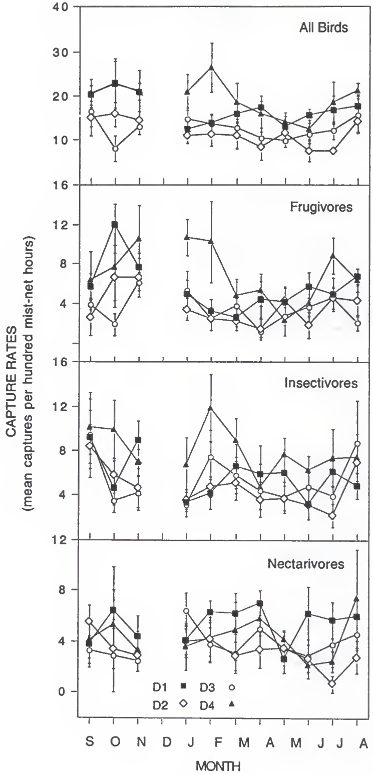


Figure 5-4. Variation in the distribution of understory birds at La Planada in relation to distance from forest edge and month. Points represent means and bars standard errors.

The distance effect was also affected by month for frugivores as shown by the significant interaction between these two factors (ANOVA, $F_{45,181} = 1.93$, $P = 0.007$; Table 5-1, Fig. 5-4). I found that capture rate of frugivores was significantly higher at D4 (mean = 8.4) than at D1 (mean = 4.7) during the dry months (Contrast of Mean Differences, $F_{1,120} = 7.3$, df = 1, $P < 0.008$) but not during the wet months. The distance x month interaction in the omnibus test was not significant for insectivores and nectarivores (Table 5-1, Fig. 5-4). However, when I tested specific hypotheses I found that capture rates of insectivores were higher at D4 (mean = 8.0 and 8.4 for dry and wet season, respectively) than at D1 (mean = 4.2 and 6.6 for dry and wet season, respectively) in both seasons (Contrast of Mean Differences, $F_{1,120} = 6.7$, $P = 0.01$). For nectarivores I found that capture rates were higher at D1 (mean = 5.6) than at D4 (mean = 3.2) only during the dry season (Contrast of Mean Differences, $F_{1,120} = 5.7$, $P = 0.02$).

The abundance of insectivores changed in old and new edges depending on the month of the year, as shown by the significant interaction between month and edge age (ANOVA, $F_{16,\ 64} = 3.24$, $P = 0.004$; Table 5-1, Fig. 5-3). Insectivores were more abundant at new edges (mean = 7.9) than at old edges (mean = 5.4) only during the wet season (Contrast of Mean Differences, $F_{1,40} = 7.0$, $P = 0.01$).

Species Level Responses

From June 1992 through August 1993 I captured 2,101 birds of 82 species. Ninety percent of the captures represented 22 species that were classified as abundant (21-50 captures) and very abundant (>51 captures) (Appendix B). Insectivores accounted for 39% of all bird captures, frugivores for 32%, nectarivores for 28%, and carnivores for 1%.

Twenty-four species and the complex Tangara spp. (which includes T. arthus, T. labradorides, and T. nigroviridis) were evaluated to establish variation in their abundance with distance from the edge. The distribution of bird captures for 17 out of the 24 common species departed significantly from a uniform distribution across the four distances (Table 5-2). Given a 10% probability of obtaining a species that shows a non-uniform distribution, it is very unlikely that 17 or more species out of 24 would have shown a non-uniform distribution just by chance alone (Binomial Test, $P = 1.6 \times 10^{-12}$). I conclude that the distribution of understory birds is affected by edges.

Based on the observed and expected cell frequencies I further divided the species exhibiting a non-uniform distribution into three groups: (1) species for which the observed number of captures at D4 was higher than expected, i.e., increasing from edge to interior, (n = 8), (2) species for which the observed number of captures at D1 was higher

Table 5-2. Distribution of common ($\geq$21 captures) understory bird species of La Planada in relation to distance from edge. Numbers are number of captures. $P < 0.1$ (*), $P < 0.05$ (**), $P < 0.01$ (***), $P < 0.001$ (****).

	Distance				G-stat	P
	D1	D2	D3	D4		
Uniform Distribution						
Allocotopterus deliciosus	13	10	11	12	0.42	ns
Euphonia xanthogaster	32	22	17	24	4.16	ns
Pipreola riefferii	7	5	4	5	0.89	ns
Tangara spp.	8	4	4	11	5.08	ns
Basileuterus tristriatus	23	14	25	20	3.54	ns
Grallaricula flavirostris	9	13	19	21	6.14	ns
Myiphobus flavicans	9	6	3	5	3.27	ns
Premnornis guttuligera	25	33	25	27	1.52	ns
Non-Uniform Distribution						
Increase from Edge to Interior						
Atlapetes brunneinucha	3	4	11	10	7.52	*
Lipaugus cryptolophus	1	2	5	8	7.78	*
Mionectes striaticollis	30	16	15	61	41.63	****
Glyphorrynchus spirurus	10	9	10	30	18.17	****
Myiotriccus ornatus	11	6	9	23	12.51	***
Premnoplex brunnescens	8	20	25	40	23.94	****
Pseudotriccus pelzelni	13	14	15	40	21.58	****
Aglaiocercus coelestis	50	53	68	85	11.82	***
Decrease from Edge to Interior						
Chlorospingus semifuscus	13	2	3	5	13.64	***
Coeligena wilsoni	42	25	18	28	10.49	**
Haplophaedia lugens	20	11	13	7	6.87	*
Ocreatus underwoodii	10	3	4	1	9.6	**
Increase at Edge and Interior						
Masius chrysopterus	37	27	25	58	17.47	****
Myadestes ralloides	25	16	9	37	20.58	****
Henicorhna leucophrys	38	19	24	34	8.19	**
Syndactyla subalaris	14	6	6	14	6.59	*
Phaetornis syrmatophorus	62	21	34	47	23.28	****

than expected, i.e., decreasing from edge to interior (n = 4), and (3) species for which the observed number of captures at D1 and at D4 was higher than the expected, i.e., increase both at the edge and forest interior, (n = 5) (Table 5-2). These patterns suggest that edges might influence the distribution of birds in complex ways, such that some species avoid edges, others are attracted to edges, and still others are influenced by factors other than distance from forest edge. This latter situation is suggested by those five species showing an increase both at forest edge and forest interior.

Fourteen species were evaluated to determine the combined effect of distance from the edge and edge age on their abundance (Table 5-3). I recognized two main groups: (1) species showing a significant interaction between distance from the edge and edge age ($G_{Heterogeneity}$, $P < 0.1$) and (2) species showing a non-significant interaction between distance from the edge and edge age ($G_{Heterogeneity}$, $P > 0.1$; Table 5-3). Within these two groups species showed different responses across the four distances depending on edge age (G_{Old} and G_{New}, $P < 0.1$; Table 5-3). Thus, the distribution of individuals within a species not only changes from edge towards forest interior but also varies with edge age.

For all species combined, I found a significant association between species abundance and distance from the edge ($\chi^2 = 24.4$, df = 12, $P = 0.02$; Table 5-4). Moreover, upon examination of the residuals I found that the

Table 5-3. Results of Replicated Goodness of Fit Test on the number of captures for understory birds at the Reserva Natural La Planada. $G_{Heterogeneity}$ (G_H), G_{Total} (G_T), G_{Old} edges (G_O), G_{New} edges (G_N). $P < 0.1$ (*), $P < 0.05$ (**), $P < 0.01$ (***), and $P < 0.001$ (****).

	df	G_H	df	G_T	df	G_O	df	G_N
Mionectes striaticollis	3	19.89****	6	61.53****	3	6.43*	3	55.07****
Myadestes ralloides	3	8.76**	6	29.31****	3	17.95****	3	13.16***
Premnoplex brunnescens	3	13.14***	6	37.08****	3	9.15**	3	27.90****
Aglaiocercus coelestis	3	6.56*	6	18.37***	3	9.74**	3	8.6**
Euphonia xanthogaster	3	13.50***	6	17.74***	3	1.22	3	16.51****
Allocotopterus deliciosus	3	1.46	6	1.88	3	0.44	3	1.43
Basileuterus tristriatus	3	2.66	6	6.19	3	1.42	3	4.77
Grallaricula flavirostris	3	0.30	6	6.42	3	3.72	3	2.71
Premnornis guttuligera	3	1.50	6	3.02	3	1.18	3	1.83
Pseudotriccus pelzelni	3	2.12	6	23.70****	3	11.64***	3	12.05***
Phaetornis syrmatophorus	3	4.24	6	27.5****	3	13.97***	3	13.56***
Masius chrysopterus	3	4.22	6	21.73***	3	7.23*	3	14.42***
Henicorhina leucophrys	3	3.72	6	11.92*	3	1.48	3	10.41**
Coeligena wilsoni	3	0.79	6	11.26*	3	8.26**	3	3.0

Table 5-4. Distribution of understory birds across the pasture forest-edge. Birds were classified according to abundance. Numbers represent number of captures. Carnivores were excluded because of small number of captures.

		Distance			
		D1	D2	D3	D4
Extremely sparse (1 capture)	All Birds	12	3	6	4
	Frugivores	5	2	0	0
	Insectivores	3	1	3	1
	Nectarivores	3	0	3	2
Very sparse (2-5 captures)	All Birds	31	11	12	14
	Frugivores	10	3	8	2
	Insectivores	9	3	5	8
	Nectarivores	11	0	1	4
Sparse (6-20 captures)	All Birds	41	32	24	43
	Frugivores	9	13	10	23
	Insectivores	17	13	9	19
	Nectarivores	15	6	4	1
Abundant (21-50 captures)	All Birds	70	39	46	75
	Frugivores	36	21	28	33
	Insectivores	34	18	18	42
	Nectarivores				
Very abundant ($\geq$51 captures)	All Birds	423	314	342	557
	Frugivores	124	81	66	179
	Insectivores	126	122	143	211
	Nectarivores	173	111	133	167

contribution of extremely sparse and very sparse species at D1 was disproportionally high. There was also a significant association between species abundance and distance from the edge for frugivores and nectarivores ($\chi^2 = 32.8$, df = 12, $P = 0.001$ and $\chi^2 = 27.0$, df = 9, $P = 0.01$, respectively; Table 5-4). An examination of the residuals for frugivores showed that (1) extremely sparse species were captured more frequently than expected at D1 than at the other three distances, (2) very sparse and abundant species were captured more frequently than expected at D3 than at the other distances, and (3) very abundant species were captured more frequently than expected at D4 than at the other distances. Among nectarivores the residuals showed that (1) very sparse and sparse species were captured more frequently than expected at D1 than to the other distances and (2) very abundant species were captured more frequently than expected at D4 than to the other distances.

Discussion

The distribution of understory birds at La Planada varied across pasture-forest edges in complex ways, not always reflecting changes due to the presence of edges. This complexity is demonstrated by (1) differences among the response variables and (2) significant interactions between distance from edge, edge age, and month. Capture rates for all birds, frugivores, and insectivores changed across the pasture-forest edge, but the same was not true for nectarivores. In my study area, and averaging over time, capture rates for all birds and frugivores showed bimodal distributions peaking, at D1 (0-10 m) and D4 (190-200 m). Capture rates for insectivores showed an abrupt increase at D4. Time since edge creation, however, had a major effect on capture rates for all birds and frugivores across the pasture-forest edge, especially at D3 (60-70 m) and D4 (Fig. 5-2). Within edges, capture rates of frugivores varied among the four distances on a monthly basis. Between edges, capture rates of insectivores varied between old and new edges on a monthly basis. In discussing these findings I will (1) compare them against results from studies conducted in other tropical areas and (2) look at possible factors that might influence the distribution of birds across pasture-forest edges.

Patterns of Bird Distribution across Edges

My results agree with those of other studies on edges in that (1) abundance (or density) of organisms changes from edge towards forest interior (Quintela 1986, Laurance 1990, Malcolm 1994), (2) functional or taxonomic groups of organisms, as well as individual species, respond in different ways to the creation of edges (e.g., Noss 1991), and (3) the magnitude and direction of the responses to the creation of edges varies depending on time since edge creation and season.

A study conducted in the Amazon showed that overall abundance of birds in forest stands increased from the edge towards forest interior (Quintela 1986; but see Kroodsma 1984 and Lopez de Casenave et al. ms for opposite results). Edge age and land use can affect the magnitude of such effects (DeGraaf 1992). At larger scales, landscape configuration determines the overall effect of edges on the distribution of organisms (Hansen et al. 1992).

I reanalyzed Quintela's data on bird captures and found that, in central Amazon, understory insectivores (Goodness of Fit Test, G = 49.6, $P < 0.001$) and frugivores increased (Goodness of Fit Test, G = 5.8, $P < 0.1$) from edge towards the forest interior (500 m from forest edge), whereas nectarivores decreased (Goodness of Fit Test, G = 7.1, $P < 0.05$). In the Chaco Argentino, bird captures of terrestrial and arboreal granivores, i.e., doves and parrots, was higher at forest edge than at forest interior (Lopez de Casenave et al. ms). Mist netting did not reveal differences among the other guilds. The Amazon site and La Planada differ markedly in their understory avifauna (Bierregard and Lovejoy 1989). Nevertheless, results of both studies show that (1) abundance of all birds, frugivores, and insectivores is highest in the forest interior and (2) abundance of nectarivores is highest at the forest edge. In both areas, pastures and second growth areas are embedded in a forest matrix (Lovejoy et al. 1986, Chapter 2).

In central Sweden, bird density across clear cut-forest edges changed over a year (Hansson 1983). Bird density was higher at the "edge" (50 m from edge), than at the forest interior (>50 m from edge) and these differences were more pronounced in the summer than in the winter (Hansson 1983). In central Florida, overall bird density was higher near the forest edge (50 m from edge) than farther away, and this difference was greater during winter than at other times of the year at east-facing edges (Noss 1991). Noss also found variability among years in the response of birds to edges. At La Planada, capture rates for all birds and for frugivores were greater at D4 (190-200 m) than at D1 (0-10 m) during dry months. Capture rates for insectivores were higher at D4 than at D1 and they did not differ between the wet and dry season. For nectarivores capture rates were higher at D1 than at D4 only during the dry season. The within-year variability in bird abundance across forest edges suggests that edges are dynamic. In addition, this variability is suggestive of possible mechanisms underlying the observed patterns.

Factors Influencing the Distribution of Birds across Edges

Environmental factors and intrinsic features of organisms may influence their distribution across edges (Wiens 1992). Most of these factors have been examined in temperate zones, especially in areas where forest fragments are embedded in an agricultural matrix. They include nest parasitism and egg predation (Gates and Gysel 1978, Wilcove et al. 1986, Andrén and Algestam 1988, Møller 1989), and predation and parasitism of adults (Wiens et al. 1985, Loye and Carroll 1995). In addition, edges can directly influence the distribution of organisms by affecting their physiological condition (Wiens et al. 1985), probability of establishment in a given area depending on home range size (Kuitunen and Mäkim 1993), and dispersal abilities.

In tropical areas there has been little effort to elucidate factors underlying changes in the distribution of animals across edges (Malcolm 1991). Some studies using artificial nests have shown that nest predation increases towards forest edges where second growth vegetation abuts undisturbed forest (Gibbs 1991, Burkey 1993). However, nest predation rates did not change across pasture-forest edges at three other sites, including La Planada (Arango 1991, Laurance 1993, C. Restrepo and C. Samper, unpublished data). In an Amazonian site, Malcolm (1991) found that the distribution of small mammals changed between "interior" and "edge" in continuous tracts of forest. These changes mirrored those in forest structure and abundance of insects, and he concluded that changes in resource levels could explain changes in small-mammal assemblages in the Amazon across pasture-forest edges.

At La Planada the distribution of frugivores might be partially influenced by the distribution of resources across the pasture-forest edge. Fruit abundance (measured as total number of fruits and as number of ripe fruits), decreased significantly from the edge towards the forest interior

(Chapter 4). Capture rates of understory frugivorous birds followed a similar trend up to 70 m from the edge. Fruit abundance (measured as total number of fruits excluding palms and as total number of fruiting individuals), differed across pasture-forest edge depending on month (Chapter 4). Frugivores, but not insectivores or nectarivores, changed in the same fashion, as indicated by the significant distance x month interaction.

Two other factors influenced the distribution of frugivores across pasture-forest edge. First, at D4 fruit abundance was the lowest, yet capture rates of frugivores were the highest. This increase in capture rates was probably influenced by the presence of two leks (*Mionectes striaticollis* and *Masius chrysopterus*) in the vicinity of D4 in one of my study edges (Hermógenes). It is impossible to tell if the establishment of these leks was related to edge creation 12 years ago. The presence of the leks, however, certainly acts as an attractor, thus affecting the distribution of *M. striaticollis* and *M. chrysopterus* in one of the edges. Second, the sharp increase in capture rates of insectivores at D4 suggests that some structural feature of the forest and/or resource covarying with structure changed at D4 and that both frugivores and insectivores responded to this. A gentler topography and the presence of larger gaps at D4 when compared to the other distances may result in changes in forest structure. Thus, as pointed out by Wiens (1992), the distribution of organisms across edges is influenced not only by distance from forest edge but also by species characteristics, such as their behavior.

The distribution of nectarivores showed a sharp decrease from edge to forest interior, even though the omnibus test was not significant. In Brazil, Quintela's (1986) data show the same trend but it was significant. In the lowlands of Costa Rica, Blake and Loiselle (1991) found that capture rates of nectarivores decreased from young second growth to old second growth to forest. In Monteverde (Costa Rica) cloud forest, Feinsinger et al. (1987) found that the frequency of visits by hummingbirds decreased from large gaps to small gaps to forest. At La Planada, the distribution of hummingbird-pollinated plants showed a significant decrease from edge towards forest interior (Goodness of Fit Test, $\chi^2 = 23.01$, df = 3, $P < 0.05$), suggesting that resources might be responsible for the observed trend in nectarivores. This at least can explain why very sparse and sparse nectarivores were captured more often at D1 than at the other distances.

CHAPTER 6

FRUGIVOROUS BIRDS IN FRAGMENTED NEOTROPICAL MONTANE FORESTS: LUMP STRUCTURE IN BODY MASS

Introduction

Transformation of tropical landscapes by humans has influenced plant and animal assemblages in many ways. Most studies have emphasized how species abundance and richness change with increasing forest fragmentation (Quintela 1986, Bierregaard and Lovejoy 1989, Klein 1989, Newmark 1991, Estrada et al. 1993, Kattan et al. 1994, Malcolm 1994, Didham, *in press*, Lynam, *in press*, Warburton, *in press*, Chapter 5) and with transformation of native forests into second growth and managed ecosystems (Holloway et al. 1992, Johns 1992, Lambert 1992, Thiollay 1992, Andrade and Rubio 1994, Escobar 1994). Results of these studies vary considerably, reflecting the complexity of relating habitat modification to biodiversity loss, but also inherent differences among study sites, and/or a mismatch between the scale of the problems being addressed and the methods used. As a consequence it has been difficult to establish patterns regarding how habitat modification and biodiversity interact and moreover, how they relate to ecosystem processes

(Vitousek 1990, Kruess and Tschnarntke 1994, Pimm and Sugden 1994, Tilman and Downing 1994, Turner et al. 1995).

Holling et al. (1995) provided a novel conceptual framework that may help integrate these issues. First, long-term research has shown that ecosystems are structured by a few processes operating at various spatial and temporal scales (e.g., Clark et al. 1979, Harris 1980, Gunderson 1992). Second, the behavior and morphology of organisms reflect the discontinuous nature of ecosystems. In particular, body mass of boreal birds and mammals was found to be discontinuously distributed, such that species of similar mass tend to aggregate or lump together (Holling 1992). By focusing on lumps, rather than species, it may be possible to detect patterns at larger spatial scales such as those defined by the impact of humans on landscapes. Third, the morphology of organisms reflects differences in landscape pattern. In particular, the distribution of body mass in boreal forest and boreal prairie birds differed (Holling 1992). By focusing on the distribution of body mass, i.e., lump structure, it could be possible to investigate the interaction between landscape pattern and the structure of animal and plant assemblages.

In this paper I ask how changes in landscape pattern affect assemblages of frugivorous birds in neotropical mountains. I concentrate on frugivorous birds because seed dispersal by birds is especially important in neotropical mountains compared to the lowlands (Terborgh 1977, Stiles

1985, Gentry 1988, Renjifo et al., *in press*), offering an opportunity to relate the process of seed dispersal to landscape pattern. I focus on mountains because natural and human disturbances have generated complex landscapes over small areas (Haslett 1994), offering an ideal opportunity to assess how changes in landscape pattern influence animal assemblages.

I make four comparisons representing two different scales of inquiry and address how the distribution of body mass, i.e., lump structure, in frugivorous birds changes from areas covered mostly by forest to areas covered by open vegetation. The first scale is defined by elevational zones within the mountains of Colombia, the second by sites within elevational zones that have been differently affected by human activities. I use body mass as an attribute that reflects information not only on life-history traits, such as dispersal (Laurance 1991, Lawton et al. 1994, Brown 1995, Gaston and Blackburn 1995), but also on foraging behavior, such as size of seeds being dispersed (Moermond and Denslow 1985).

Methods

Study Area

My study focused on the Andes of Colombia, South America. This system consists of three mountain ranges of different geological origin, each running in a S-N direction

(Irving 1975). I defined montane habitats as those above the 800 m topographic contour line (Fig. 6-1). In the absence of human disturbance this region would be covered by forest except for the páramo and small areas affected by rain shadows (Cuatrecasas 1958). Forest composition, structure, and physiognomy change along the mountains from the complex lowland tropical forest to the simpler páramos (Cuatrecasas 1958, Espinal et al. 1977).

The area encompassed by this study represents less than 35% of the total area of Colombia (1,380,000 km^2) yet harbors one of the richest biotas not only of this country but of the neotropics (Duellman 1979, Henderson et al. 1991, Gentry 1992a,b, Renjifo et al. *in press*). It has been postulated that the elevated levels of diversity and endemism of this area are the result of an intense disturbance regime (Gentry 1992a, J. Luteyn *pers. comm.*). A complex topography and geology, combined with high precipitation, generates landslides, mud flows, avalanches, and volcanic eruptions, which continuously transform these mountains (Mejía et al. 1994, Velásquez et al. 1994).

Superimposed on the natural disturbance regime is one generated by human activities. At least 50 per cent of the total population of Colombia (37 million people) has settled in montane areas (Banguero 1993). Presently, less than 30 percent of this area is covered by forest, most of which is found either at elevations >2,500 m or on wetter slopes of the cordilleras (Cavelier and Etter, *in press*). The remaining

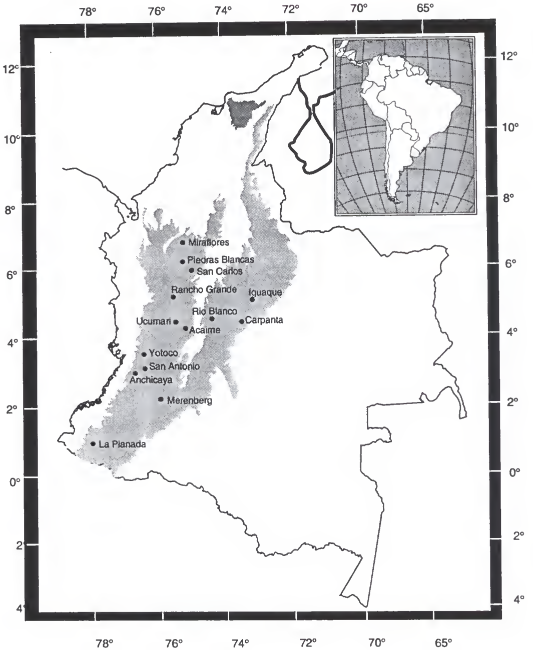


Figure 6-1. Montane habitats of Colombia (≥800 m) showing the location of sites included in this study.

area has been transformed into pastures, cultivated fields, coffee and tree plantations, and urban areas. A recent surge in demand for opium derivatives has prompted forest clear-cutting at higher altitudes to grow poppy (Papaver somniferum; Cavelier and Etter, *in press*).

Frugivorous Birds

I included all species reported to consume fruits and/or seeds to any degree (Fitzpatrick 1980, Hilty and Brown 1986, Isler and Isler 1987, Renjifo 1988, Ridgely and Tudor 1989, Stiles and Skutch 1989, Fjeldså and Krabe 1990, Velásquez 1992, Arango 1993, 1994, Ridgely and Tudor 1994, L.M. Renjifo and C. Restrepo *personal observations*) and found at an elevation ≥800 m. Thus, my data combine seed dispersers and seed consumers.

Body mass data were obtained from published records (Goodwin 1976, Isler and Isler 1987, Stiles and Skutch 1989, Dunning 1993, del Hoyo et al. 1992, Arango 1993), museum specimens (Colección de Ornitología, Universidad del Valle, Cali, Colombia), and my own field observations. For bird species that I could not obtain mass measurements, I averaged the available mass for congeners of the same length. I could not estimate body mass for a small fraction (2%) of the species and these were not included in the analyses.

To explore the relationship between body mass and landscape pattern along the elevational gradient, I classified birds into four groups based on their elevational ranges: upper lowland (from ca. 800 m to 1,500 m), lower montane (from ca. 1,500 m to 2,400 m), upper montane (from ca. 2,400 m to 3,400 m), and páramo (from ca. 3,400 to 4,800 m) species (Table 6-1). Note that some species fell in more than one elevation zone and were entered into the analyses two or more times. Elevational zones follow Chapman (1917). Elevational ranges were taken from Hilty and Brown (1986).

To explore the relationship between body mass and landscape pattern along a gradient of land-use, I obtained bird inventories for 18 sites (Table 6-1). All inventories were conducted by experienced ornithologists over periods of ≥1 yr and included visual, auditory, and mist netting observations. I believe these lists represent unbiased and fairly complete inventories, so additions would have little influence on the results. The 18 sites were grouped according to elevational zone and type of land use. Within each comparison I arranged sites from those covered mostly by forest to those covered by open vegetation (Table 6-1). This work relies on two assumptions. First, there is a common pool of species for elevational zones and sites, but historical, geographical, and climatic events, and more recently human activities, have determined the set of species found today at any one site. Second, within elevational zones the less disturbed sites represent the conditions that existed at the other sites prior to human intervention.

Table 6-1. Sites included in this study.

Site	Coordinates	Elevation (m)	Life Zone^1 *sensu* Holdrige	Land Use^2	References
Upper Lowland (600/800 to 1,400/1,600 m)					
Anchicaya-Alto Yunda, PNN Farallones de Cali (AN)	3°32'N 76°48'W	1,050	TP-rf	F/F, SG	7, 29
Reserva Forestal Yotoco (YO)	3°52'N 76°33'W	1,500	TP-df/mf	F/P, CT	14, 31
Represa San Carlos (SC)	6°13'N 74°51'W	750	TP-mf/wf	SG^a/F,P	23
Finca La Esmeralda (LE)		1,250	TP-wf	CT/CT, P	4
Finca El Ocaso (EO)		1,000	TP-wf	P/F^b	4
Lower Montane (1,400-1,600 to 2,300/2,600 m)					
Reserva Natural La Planada (LP)	1°10'N 78°00'W	1,800	TP-rf	F/SG	6, 15, 19,27
Parque Regional Ucumari, Ucumarí Bajo (UB)	4°47'N 75°32'W	1,850	TLM-wf	F/SG, TPE^{c,e}	6, 13, 16, 26, 28
Bosque Protector San Antonio (SA)	3°29'N 76°38'W	2,000	TLM-wf	F/SG, U	6, 9, 10, 26, 27, 30
Empresas Publicas de Manizales (RB)	5°28'N 75°32'W	2,400		SG,TPN^d, P	22, 25, 28
Finca Merenberg (ME)	2°14'N 76°08'W	2,300	TLM-wf	P/F	6, 17, 20, 32
Represa Miraflores (MI)	6°45'N 75°20'W	2,130	TLM-wf	SG/P	5
Finca Rancho Grande (RG)	4°36'N 74°20'W	1,700		P/CT,SG,U	12
Finca Mirador, Munchique (MU)	2°30'N 76°59'W	2,300	TLM-wf	TPE^e/SG, P	11
Piedras Blancas (PB)	6°18'N 75°30'W	2,350	TLM-wf	TPE^e	8
Upper Montane (2,300/2,600 to 3,100/3,400 m)					
Reserva Natural Carpanta-Estacion Sietecuerales (CA)	4°34'N 73°41'W	2,700		F/SG	2
Reserva Natural Alto Quindio Acaime (AC)	4°37'N 75°20'W	2,800	TM-wf	SG/TPN^d, F, P	3, 18
Parque Regional Ucumari, Ucumarí Alto (UA)	4°47'N 75°32'W	2,500		SG/TPN^d, F, P	6, 13, 16, 21, 26, 28
Santuario de Flora y Fauna Iguaque-Cañon Mamarramos (IG)	5°40'N 73°30'W	2,600	TLM/TM-mf	SG/P, F^a	1, 21, 24,25
Paramo (3,100/3,400 to 4,800 m)					

Table 6-1. continued

References: (1) Acevedo (1987), (2) Andrade (1993), (3) Arango (1994), (4) Corredor (1989), (5) Cuadros (1988), (6) Gentry (1992a), (7) Hilty (1980), (8) Johnels and Cuadros (1986), (9) Kattan et al. (1984), (10) Kattan et al. (1994), (11) Mondragón (1989), (12) Munves (1975), (13) Naranjo (1994), (14) Orejuela et al. (1979), (15) Orejuela and Cantillo (1990), (16) Rangel (1994), (17) Rangel and Espejo (1989), (18) Renjifo (1988), (19) Restrepo (1990), (20) Ridgely and Gaulin (1980), (21) Rosas (1986), (22) Uribe (1986), (23) Velasquez (1992), (24) Velez (1987), (25) N. Arango, personal communication, (26) G. Kattan, personal communication, (27) C. Restrepo, personal observation, (28) L. M. Renjifo, personal observation, (29) S. Hilty, unpublished list, (30) G. Kattan, H. Alvarez,and M. Giraldo,unpublished list, (31) H. Alvarez, unpublished list, (32) G. Kattan, H. Alvarez, and E. Buttkus, unpublished list.

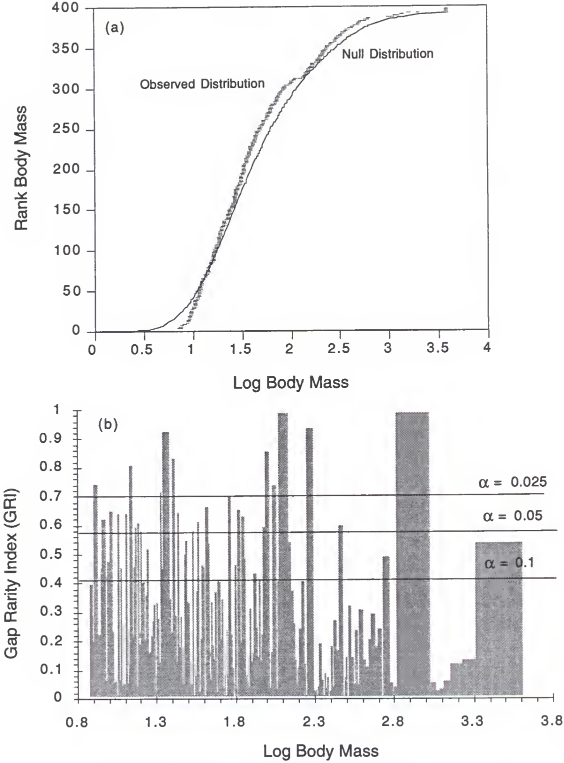
[1] Life zone: Tropical premontane dry forest (TP-df), Tropical premontane moist forest (TP-mf), Tropical premontane wet forest (TP-wf), Tropical premontane rain forest (TP-rf) Tropical lower montane wet forest (TLM-wf), tropical lower montane moist forest (TLM-mf), tropical montane wet forest (TM-wf).

[2] Land Use: (F) native forest, (SG) second growth, (P) pasture, (CT) shaded coffee plantation, (TPE) tree plantations with exotic species, (TPN) tree plantations with native species, (U) weekend cottages. [a] selectively logged native forest, [b] native forest dominated by the Giant Bamboo, *Bambusa guadua*, [c] plantations with *Fraxinus sinensis*, [d] plantations with *Alnus acuminata*, [e] Plantations with *Pinus patula* and *Cupressus lusitanicus*.

Data Analysis

I used the Lump Analysis (LA_{GRI}) technique to analyze the data (GaP Detector 2.1). This technique is being developed by P. Marples, Arthur Marshall, Jr. Lab, Department of Zoology, University of Florida. LA_{GRI} tests whether breaks in an observed frequency distribution of an attribute occur by chance alone due to sampling error (Fig. 6-2a). It relies on the generation of a continuous, unimodal distribution from input data (in this case, body mass) and the detection of gap rarity indexes, or GRI-values within the data set. The unimodal distributions are derived using the smallest normal kernel estimate (h) that smoothes a frequency distribution into an unimodal continuous distribution (Silverman 1986). GRI-values are derived by calculating the absolute differences between contiguous rank size-ordered data points for the observed and expected distributions. The GRI-values for a given data set are compared against a critical value (GRI_{crit}), and those that exceed that value define a significant break (gap) in the observed frequency distribution at the indicated alpha level (Fig. 6-2b), the size of the observed data set (N), and the ratio between the size of the observed data set and the mean size of all the data sets that are compared simultanously (rj). All body masses between two contiguous gaps define an aggregate of species or lump. Calculations were based on $\log_{10}$-transformed

Figure 6-2. Lump Analysis of body mass for Colombian upper lowland tropical frugivorous birds (a) body mass distribution vs. rank order and (b) rank size-ordered body mass distribution vs. gap rarity indexes (GRI-values). In(b) potential gaps between the lumps are represented by GRI-values that exceed the criterion lines (alpha values).


(a)
Observed Distribution
Null Distribution
Rank Body Mass
400
350
300
250
200
150
100
50
0
0
0.5
1
1.5
2
2.5
3
3.5
4
Log Body Mass
(b)
Gap Rarity Index (GRI)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
α = 0.025
α = 0.05
α = 0.1
0.8
1.3
1.8
2.3
2.8
3.3
3.8
Log Body Mass

body masses.

Sample size strongly influences lump structure. In data sets with a large number of observations a small value of alpha might reveal a strong pattern of gaps whereas a large value might reveal a weak pattern of lumps especially at the lower end of the body mass range (Fig.2b). In this situation, reducing alpha reduces the probability of detecting gaps that might not exist (reduction of Type I error). In small data sets a small value of alpha might not reveal any pattern whereas a large alpha value might reveal strong pattern. In this situation, increasing alpha reduces the probability of not detecting gaps that exist (reduction of Type II error). Thus, the gap/lump structure of a given data set is determined by the chosen alpha level (Fig. 6-2b).

This interplay between sample size and the two types of statistical error should be taken into account when comparing multiple data sets. Lipsey (1990) gives an excellent discussion of the importance of using different values of alpha when detection of pattern is important. In this paper and for simplicity I kept the alpha level constant within each comparison. Depending on the data sets I used alpha levels of 0.05 (within comparison average sample size $\geq$81, range 30-395) and 0.1 (within comparison average sample size <81, range 30-141).

I set up nested comparisons and derived four continuous unimodal distributions. The four elevational zones were compared using a null distribution generated from the complete data base on frugivorous montane birds. The sites within a elevational zone were compared using a null distribution generated from the database on frugivorous birds for the corresponding zone.

How to interpret a lump analysis

The main results of the lump analysis are summarized in two related figures, depicting the distribution of gaps and lumps. The first illustrates the distribution of GRI-values against body mass (Fig. 6-2b), while the second, which is derived from the first, depicts the distribution of lumps and gaps for the various data sets that are being compared simultaneously (e.g., Fig. 6-3). In this paper I report only the latter. Lump structure for a given data set can be described in terms of the number and size of the lumps and the proportion of species falling within specific lumps. Lump structure for multiple data sets can be described in terms of the correspondence between the position of lumps and gaps. Presently, P. Marples is developing a procedure that will allow quantitative testing of the lump and gap correspondence. In this paper the comparison will be qualitative.

The size of the lumps represents the ranges of body mass that do not exhibit discontinuities at a given alpha level. The number of species that fall within a lump are represented as the proportion of the total number of species of the corresponding data set. In the figures depicting the distribution of lumps the proportions are represented by different shades of gray (e.g., Fig. 6-3). Thus the size of the lump does not represent the proportion of species falling within them, but rather the size range of birds involved.

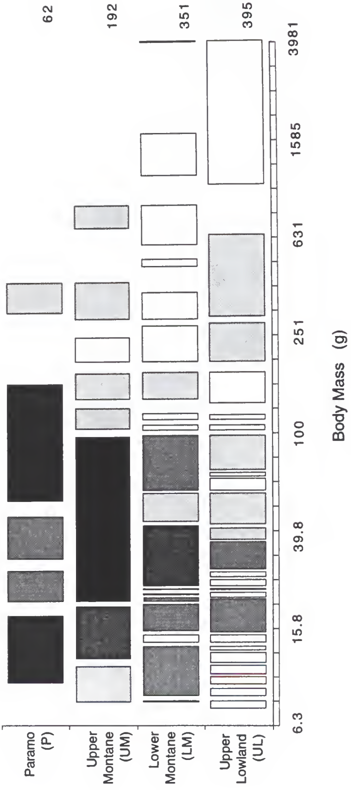
Results

Elevational Zones and Body Mass Distribution

I established the lump structure of bird assemblages for the four elevational zones using an alpha = 0.05 and found that the number of lumps decreased from the upper lowland (24 lumps) to the páramo zone (5 lumps) (Fig. 6-3). Most lumps were lost from the upper range (>316 g) and few from the lower range (<10 g) of body mass. Lumps at both extremes contained the lowest proportion of species for the upper lowland, lower montane, and upper montane zones but not for the páramo.

The lump structure of the upper lowland and lower montane zones showed striking similarities in regard to the position of gaps and lumps in the body mass range of 12-575 g. However, the proportion of species in these lumps differed between the two zones. Lump structure of the upper montane zone resembled that of the upper lowland and lower montane zones in the body mass range of 83-316 g but not above or below these figures. Finally, the páramo zone shared only one lump (>301 g) with the other three zones.

Figure 6-3. Lump structure of Colombian montane frugivorous birds according to elevational zone from forest (bottom) to paramo (top). Upper lowland (UL), lower montane (LM), upper montane (UM), and páramo (P). Each box represents a lump and the space between the boxes represent gaps in the distribution of body mass. The different shades indicate the proportion of species falling within lumps: (1) 0-5, (2) 5-10, (3) 10-20, (4) 20-30, (5) 30-45, (6) 45-60, and (7) 60-100 % of species. Vertical lines represent 0-5% of species. Numbers on the right side represent number of species for the corresponding data set.


Paramo (P)
Upper Montane (UM)
Lower Montane (LM)
Upper Lowland (UL)
62
192
351
395
6.3
15.8
39.8
100
251
631
1585
3981
Body Mass (g)

Sites and Body Mass Distribution

Upper lowland zone

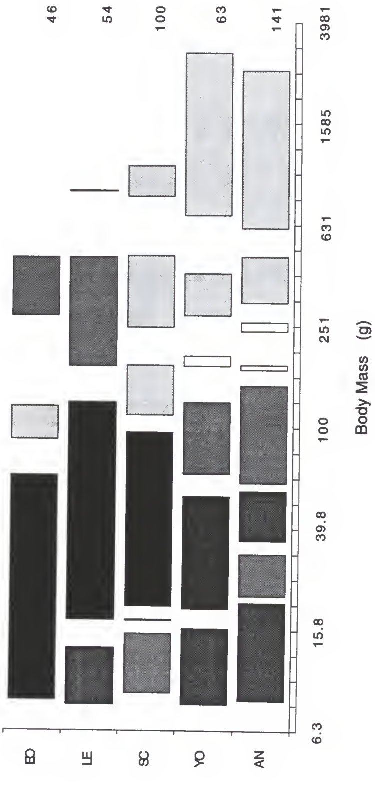
The number of lumps detected at an alpha = 0.05 decreased from the site covered extensively by forest, Anchicaya (AN, 8 lumps), to that site dominated by pastures, El Ocaso (EO, 3 lumps) (Fig. 6-4). The lumps that were lost were at the upper end of the range of body mass (>316 g); none was lost at the lower end.

The lump structure of two pairs of sites, Anchicaya (AN)/Yotoco (YO) and San Carlos (SC)/La Esmeralda (LE), exhibited the closest similarities in regard to the position of gaps and lumps, even though AN and SC have twice as many species as YO and LE, respectively (Fig. 6-4). The similarities occurred almost over the entire range of body mass. On the other hand the lump structure of LE and EO showed important differences, even though these two sites have a similar number of species and are separated only by 7 km.

Lower montane zone

The number of lumps decreased from sites covered extensively by forest (La Planada (LP), Ucumarí Bajo (UB), and San Antonio (SA), average = 8 lumps) to sites in which the original forest has been replaced by orchards (Río Grande, RG), and forestry plantations of exotic species (Munchique, MU and Piedras Blancas, PB) (average 4 lumps)

Figure 6-4. Lump structure of Colombian frugivorous birds from sites covered mostly by forest (bottom) to sites highly transformed by human activities (top) within the upper lowland zone. Anchicaya (AC), Yotoco (YO), San Carlos (SC), La Esmeralda (LE), El Ocaso (EO). Each box represents a lump and the space between the boxes represent gaps in the distribution of body mass. The different shades indicate the proportion of species falling within lumps: (1) 0-5, (2) 5-10, (3) 10-20, (4) 20-30, (5) 30-45, (6) 45-60, and (7) 60-100 % of species. Vertical lines represent 0-5% of species.
Numbers on the right side represent number of species for the corresponding data set.

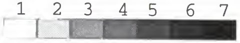

EO
LE
SC
YO
AN
46
54
100
63
141
6.3
15.8
39.8
100
251
631
1585
3981
Body Mass (g)

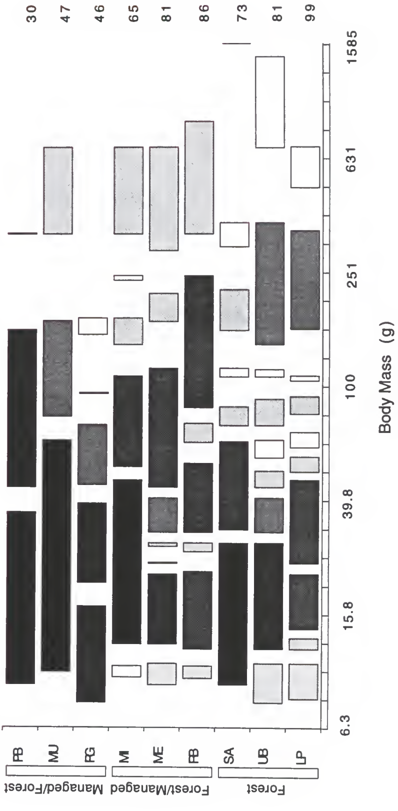
(alpha = 0.1) (Fig. 6-5).

I grouped the lower montane sites according to major types of land use to describe patterns in lump structure. Three sites are covered extensively by forest in which second growth (LP), second growth and forestry plantations (UB), and second growth, pastures, and weekend cottages (SA) cover less than 50% of land (Table 6-1). The lump structure of LP and UB, two sites differing in the number of species, is similar almost over the entire range of body mass. The lump structure of SA showed similarities with UB in the body mass range of 63-313 g, but also differences below 63 g. This occurred, even though both sites had a similar numbers of species (Table 6-1).

Three sites are covered half by native forests and half by pastures (Merenberg, ME), second growth and selectively logged forests (Miraflores, MI), and tree plantations established for watershed restoration (Río Blanco, RB). The lump structure of RB and ME showed similarities below 39 g and above 301 g and they differed greatly from that of MI almost over the entire range of body mass. In the last three sites the native forest has been replaced almost entirely by coffee plantations and orchards (Río Grande, RG) and tree plantations of exotic species for wood production (Munchique, MU and Piedras Blancas, PB). RG and MU showed a different lump structure even though they have the same number of species. The lump stucture of MU and PB was very similar, but the lump representing birds >398 g in PB was much smaller

Figure 6-5. Lump structure of Colombian frugivorous birds from sites covered mostly by forest (bottom) to sites highly transformed by human activities (top) within the lower montane zone. La Planada (LP), Ucumarí Bajo (UB), San Antonio (SA), Miraflores (MI), Merenberg (ME), Río Blanco (RB), Rancho Grande (RG), Munchique (MU), and Piedras Blancas (PB). Each box represents a lump and the space between the boxes represent gaps in the distribution of body mass. The different shades indicate the proportion of species falling within lumps:(1) 0-5, (2) 5-10, (3) 10-20, (4) 20-30, (5)30-45, (6) 45-60, and (7) 60-100 % of species. Vertical lines represent 0-5% of species. Numbers on the right side represent number of species for the corresponding data set.



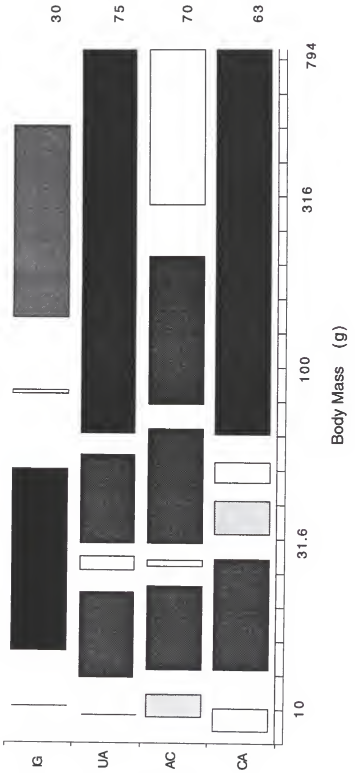

Managed/Forest
Forest/Managed
Forest
FB
MU
RG
M
ME
FB
SA
UB
LP
6.3
15.8
39.8
100
251
631
1585
Body Mass (g)
30
47
46
65
81
86
73
81
99

than the same one in MU.

Upper montane zone

I did not find marked variation in the number of lumps among the four sites when using an alpha = 0.1. Iguaque (IG) the most disturbed site, showed the smallest number of lumps (4 lumps) compared to the remaining three sites (5 lumps) (Fig. 6-6). Lumps at the upper end of the body mass range for two sites, Carpanta (CA) and Ucumarí Alto (UA), showed a high proportion of species but the contrary was true for the other two sites, Acaime (AC) and IG. More interesting, however, was the pattern of the lumps at the lower end of the body mass range (<12 g). They consistently decreased in size and in the proportion of species falling within them. Carpanta (CA), the least disturbed site, is covered by native forest and second growth and its lump structure differed from that of AC and UA particularly for species with a body mass >25 g. It is noteworthy that the highest proportion of species in CA was found in the lump representing species >63 g. For little disturbed sites at the other elevational zones those lumps representing the largest birds within the observed range of body mass always contained the smallest proportion of species. The lump structure of AC and UA was very similar. These two sites were planted with native trees in an effort to restore land previously used for cattle ranching (Table 6-1). Finally, IG showed the most conspicuous differences in regard to the position of lumps and gaps when compared regard to the position of lumps

Figure 6-6. Lump structure of Colombian montane frugivorous birds from sites covered mostly by forest (bottom) to sites highly transformed by human activities (top) within the upper montane zone. Carpanta (CA), Acaime (AC), Ucumarí Alto (UA) , Iguaque (IG). Each box represents a lump and the space between the boxes represent gaps in the distribution of body mass. The different shades indicate the proportion of species falling within lumps:(1) 0-5, (2) 5-10, (3) 10-20, (4) 20-30, (5) 30-45, (6) 45-60, and (7) 60-100 % of species. Vertical lines also represent 0-5% of species. Numbers on the right side represent number of species for the corresponding data set.


IG
UA
AC
CA
30
75
70
63
10
31.6
100
316
794
Body Mass (g)

and gaps when compared to the other sites.

Discussion

In part because of the exploratory nature of this work, and in part because of the early stage of development of the techniques to test ecosystem "lumpiness", my interpretation of the results are intended as hypotheses rather than conclusions. By exploratory I mean that I made use of information that was already available and thus could not control for many factors that might confound the results, including size of the area surveyed, hunting, and differences in vegetation types. However, the repetition of some patterns among my four analyses suggests that local differences in assemblages of frugivorous birds might be overridden by general processes that impose structure on the landscape.

Patterns in Lump Structure

In general, the number of lumps, i.e., aggregates of species having a similar body mass, decreased from areas covered by continuous native forest to areas where forest has been replaced by simpler vegetation types. It can be argued that this trend simply reflects a decrease in the number of species which in turn may reflect a decrease in habitat complexity (e.g., Karr and Roth 1971, Terborgh 1977). That is, lump structure reflects biases resulting from sampling procedures. Several of my data sets, however, did not exhibit this linear relationship. For instance, some pairs of sites (e.g., Merenberg/Ucumarí Bajo and Río Grande/Munchique) had a similar number of species and yet showed a different number of lumps. Others (e.g., Anchicaya/Yotoco, San Carlos/La Esmeralda, and Carpanta/Ucumarí Alto) had a different number of species and yet showed a similar number of lumps. A close examination of the information available for the sites revealed important structural differences between members of a pair of sites for the former whereas the same was not true for the latter (Table 6-1). This indicates that lump structure of body mass in frugivorous birds reflects to some degree the structure of landscapes.

Major changes in lump structure in terms of the persistence of lumps occurred at the upper and lower ends of the range of body mass. Lumps representing the largest bird species were lost when moving from areas covered mostly by native forest to areas where the forest has been replaced by páramo (elevation zones) and pasture (sites within the upper lowland zone). The same trend was found for small birds in the upper montane zone. In the lower montane zone there was no clear trend regarding the lumps that disappeared along the gradient of land-use.

The pattern described above may be related to the proportion of species falling within lumps. Lumps representing the largest birds contained the smallest proportion of species for the observed range of body mass for any elevational zone and sites within the upper lowland zone. Conversely, lumps representing the smallest birds contanined the smallest proportion of species for the observed range of body mass for sites within the upper montante zone. Lump structure in terms of the persistance of lumps and proportion of species falling within them was variable for sites in the lower montane zone. This indicates that lumps representing the smallest and/or largest species of frugivorous birds are the ones most prone to disappear as the native forest is fragmented and replaced by more simple ecosystems. Examples of more simple ecosystems are the paramo, along the elevational gradient, and managed ecosystems such as forestry plantations and pastures, along the gradient generated by human disturbance (Table 6-1).

I found that gaps and lumps persisted among sites representing similar landscapes but that lumps fused, broke down, or disappeared among sites representing different landscapes. This indicates that gaps in the distribution of body mass are being closed and opened probably as a result of the replacement of species (elevational zones) and local extinctions and invasions by species that were formerly absent or rare in a site. It has been well documented that species distribution changes over different spatial and temporal scales (Terborgh 1971, Hooghiemstra 1984, Gentry 1992a) and particularly relevant to this study are those changes occurring in the distribution of species as a consequence of human activities on the landscape (Pacheco et al. 1994, Lynam, *in press*).

Causes of Lump Structure

The comparisons that I set up among elevational zones and among sites within elevational zones represent two different scales of inquiry, yet produced similar results. Elevational zones and sites within elevational zones were arranged from those covered mostly by native forest to those in which the native forest has been replaced by open vegetation (páramo) or managed ecosystems (e.g., pastures and forestry tree plantations) in which scattered fragments of native forest remain. Thus, changes in lump structure seem to reflect a common causality best explained by the complexity of landscapes in terms of the vertical and horizontal structure of the vegetation. My proposition is supported by work done in other regions (Thiollay 1992, Lescourret and Genard 1994).

Vertical structure of the forest, including height of the vegetation and diversity of growth forms, is simpler as one moves from the lowlands to the páramos or from forest to pastures. Along the elevational gradient, fog, air temperature, and radiation are proximate factors that explain changes in the vegetation structure (Leigh 1975, Grubb 1977). Along the gradient of land-use, soil and rainfall distribution are proximate factors that explain changes in the structure of the vegetation (e.g., Holdrige et al. 1971).

In addition, within forest fragments wind shear-forces, atmospheric humidity, and soil moisture can alter the vertical structure of vegetation (Esseen 1994, Laurance 1994, Kapos et al., *in press*). Horizontal structure refers to the spatial array of vegetation types that results from changes in abiotic conditions or disturbance (Wiens et al. 1985). In Colombia, horizontal structure of the vegetation is simpler as one moves from the lowlands to the páramo or from little to highly modified landscapes. At lower and middle elevations, landslides generate spatial heterogeneity locally (Gardwood et al. 1979, Mejía et al. 1994, Velásquez et al. 1994). At higher altitudes, however, changes in climate and soil conditions determine the presence of forest and páramo (Cuatrecasas 1958, Espinal et al. 1977). Along the gradient of land-use, abiotic and socioeconomic factors determine not only rates of deforestation but also the matrix in which forest fragments are embedded.

Examination of the results for two sites in the lower montane zone, Río Grande and Munchique, may help understand how vertical and horizontal structure interplay and how they relate to lump structure. Río Grande and Munchique represent highly modified landscapes where fragments of degraded native forest are interspersed with orchards and pastures (RG) and pine plantations (MU) (Munves 1975, Mondragón 1989). In these two sites horizontal structure of the vegetation is similar. The same is not true, however, for vertical structure which if sampled over several points along transects would show a greater variability at RG than at MU. Even though the two sites have a similar number of species, RG has more lumps, and the species are more evenly distributed among lumps, than in MU (Fig. 6-5).

I do not know yet, on a quantitative basis, how vertical and horizontal structure interact to produce changes in lump structure of animal and plant assemblages or if they entrain some other feature of landscapes to which frugivorous birds are responding. Other features include size of fruit patches and of seeds, the latter representing a measure of both the dispersal and regeneration mode of plants (Salisbury 1974, Hughes et al. 1994, Osunkoya et al. 1994). To my knowledge there is no published account relating changes in seed size to altitude in tropical ecosystems. However, in a lowland neotropical site Martin (1975) found that mean size of seeds was smaller in second growth areas, compared to mature forest.

A Model Linking Lumps and Species Diversity in Landscapes

My results showed relationships between the number of lumps and the number of species along a gradient of structural complexity of landscapes. In addition, they hint at a relationship between lump structure and the resilience of ecosystems. Resilience as defined by Holling (1973) is a measure of the amount of disturbance and/or change that an ecosystem can absorb before turning into a different one.

These findings are summarized in a model (Fig. 6-7) where the triangles represent different ecosystems arranged from the most complex (top) to the simplest (bottom), such as elevational zones along an altitudinal gradient or types of land use along a gradient of human disturbance. The arrangement of the triangles along a diagonal line reflects the general trend showing a decrease in the number of lumps with a decrease in the number of species. Ecosystems were depicted as triangles to reflect the same general trend but this time historical, climatic, edaphic factors, and recently human activities, contribute to the within ecosystem variability.

In a given ecosystem, lump structure (vertical dimension of each triangle), defined by the number of lumps, can remain relatively unchanged in spite of differences in the number of species among sites (horizontal dimension of each triangle). In my data sets, such changes were associated with changes in species numbers within a given type of land use. However, as one approaches the apex of each triangle the probability that dramatic changes in lump structure will take place increases even though species numbers can remain relatively unchanged (vertical lines) (Fig. 6-7). In my data sets, such changes were associated with changes in land use. Each jump into successive ecosystems (from top to bottom) is accompanied by a reduction both in the number of species and the number of lumps.

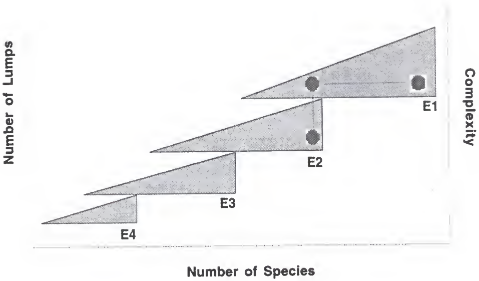


Figure 6-7. Relationship between species richness and lump structure in landscapes of variable complexity. Triangles represent ecosystems from the most complex (E1) to the simplest (E4). Points represent changes in the number of species within and between ecosystems.

The above model generates a set of testable hypotheses that could contribute to our understanding of how landscape pattern, biodiversity, and ecosystem processes interact at large scales. First, there is a threshold in species numbers below which lump structure changes dramatically, as indicated by a decrease in the number of lumps. Second, lump structure is maintained by the persistance of some species that might function as attractors. Third, lump structure of plant and animal assemblages reflects the resilience of a given ecosystem. The removal of species in ecosystems depicted by the top triangles may have a lesser impact on lump structure than the removal of species in ecosystems depicted by the the bottom ones.

Natural and human disturbances, either alone or in concert, can affect landscapes from hundreds of meters to hundreds of kilometers. The inherent complexity of ecological systems defined by this spatial domain has called for new approaches and methods. Rather than concentrating on individual parts, these new lines of inquiry concentrate on aggregates of parts and key processes that structure ecosystems (Turner et al. 1995, Holling et al. 1995). The "lump" approach represents one of these new lines of inquiry.

General Implications

In the mountains of Colombia, changes in landscape structure have dramatic consequences on assemblages of frugivorous birds. Big changes in land use result in the disappearence of lumps or complete suites of species with similar mass. The disappearence of particular lumps in body size of frugivorous birds in neotropical montane ecosystems may reflect important changes in seed dispersal and thus regeneration trajectories of vegetation after disturbance. There is some indication that assemblages of neotropical montane frugivorous birds, depending on degree of habitat modification, are robust to human disturbance. This is based on the fact lump structure varied little between similar sites that differ in the number of species. The fragmentation and transformation of neotropical montane ecosystems does not seem to generate the same patterns in assemblages of frugivorous birds in low to middle high altitudes and high altitudes. This may have important consequences for the conservation and management of ecosystems along the altitudinal gradient.

CHAPTER 7
CONCLUSIONS

Studies designed to evaluate "edge effects" (*sensu* Harris 1984) have emphasized the maximum distance at which changes induced by edge creation are apparent within stands (e.g., Williams-Linera 1990, Blanchard 1992, Chen et al. 1992). Variation among studies is enormous in terms of "depth" of edge effects due to variation in edge features (e.g., Kroodsma 1984, Quintela 1986, Noss 1991, DeGraaf 1992) and to the fact that abiotic factors and organisms show different responses to the creation of edges.

I have avoided in my work the use of the term "edge effects" (Harris 1984). This is partially due to the complexity of the responses that fruits and birds showed to the presence of edges at my study site. Equally important was the realization that "edges" are not isolated and fixed elements in landscapes. They seem to regulate what happens between the forest and the nearby disturbed area, and at the same time they connect different elements of landscapes. This is particularly true in the La Planada region, where transient corn fields, pastures, and second growth areas of various ages are embedded in a forest matrix. "Edge dynamics" reflects the influence of edges on plant and animal assemblages more accurately than "edge effects".

The different responses shown by the four variables describing fruit abundance in the understory and by the different plant species suggest differences in edge "penetrability" to the factors regulating fruit production and seed movement. These differences were manifested across the four distances within the edges but also among new and old edges. Steep and permanent gradients from edge towards forest interior may suggest low penetrability. Conversely, shallow and more variable gradients may suggest high penetrability.

My results showed that fruit abundance is influenced by edges but that the exclusion of certain groups of plants produces different results. This provided insight regarding the scales at which edges influence fruit abundance. Future studies aimed at understanding the role of edges in landscapes should take the "scale" issue into consideration.

One important finding is that related to the distribution of sparse species of plants and birds in the immediate vicinity of pasture-forest edges. These species may persist and take advantage of changes taking place at either side of the edge depending on habitat preferences. As more forest is felled, species characteristic of large disturbed areas may establish in the recently disturbed area. On the other hand, as pastures and fields are left abandoned species characteristic of forest may establish there. Thus, edges might function as "stepping stones" to recolonization at both sides and as elements that connect, rather than separate, different elements of the landscape in the La Planada region.

I argue that a "lump" analysis (Chapter 6) can help understand the role of edges in landscapes. Edges when viewed on a scale larger than that of a forest stand and the nearby disturbed area show a tremendous variability. A single measure of landscape complexity as proposed in Chapter (6), which combines a horizontal and vertical component of landscapes, can summarize edge features in a given area. By trying to recognize patterns at large scales, such as those defined by the impact of humans on landscapes, we might be able to find a relationship between landscape pattern, processes affecting landscape pattern, and the organisms that live in them. This might be particularly true for the study of fruit-frugivore interactions, since one outcome of such interactions is seed dispersal. Landscape pattern is not only changed as a consequence of disturbance; it is also changed in fundamental ways by the process of seed dispersal. In areas that are highly diverse such an approach might be the best to understand the magnitude of the impact that humans have on the biota.

APPENDIX A
PLANT SPECIES FRUITING IN THE UNDERSTORY OF THE RESERVA NATURAL LA PLANADA

APPENDIX A
PLANT SPECIES FRUITING IN THE UNDERSTORY OF THE RESERVA NATURAL LA PLANADA (SEPTEMBER 1992-AUGUST 1993)

Habitat (H): forest (F), treefall gaps (G), large-disturbed areas, including second growth, road sides (LD). Abundance of fruiting individuals at the edges included in this study (AB): very abundant (VA), abundant (A), sparse (S), very sparse (VS), extremely sparse (ES). Seeds found in bird droppings (BD). Letters followed by numbers indicate collection number.

FAMILY	SPECIES	H	AB	BD
Old and New Edges				
Araceae				
	Anthurium andinum Engl.	F	S	BD
	Anthurium carchiense Croat	LD	A	
	Anthurium cf. *marmoratum* Sodiro	F	A	
	Anthurium cf. *melampyi* Croat	F	VA	BD
	Anthurium cf. *pulverulentum* Sodiro	F	A	
	Anthurium lancea Sodiro	F	VS	
	Anthurium longicaudatum Engl.	F	S	BD
	Anthurium membranaceum Sodiro	LD	VA	BD
	Anthurium mindense Sodiro		S	
	Anthurium ovatifolium Engl.	F	S	BD
	Anthurium sp.	LD	VS	BD
	Anthurium terracolum Croat	F	S	
	Anthurium trinerve Mig.	F	VS	
	Anthurium umbraculum Sodiro	F-LD	VA	BD
	Anthurium umbricolum Engl.	F	A	BD
	Anthurium versicolor Sodiro CR 556, CR 583, CR 670, CR 791	F	VA	

	Monstera sp.	F	VS	
Araliaceae				
	Schefflera aff. *lasiogyne* Harms		VS	
	Schefflera *lasiogyne* Harms	LD	VS	BD
Arecaceae				
	Aiphanes sp.	F	S	BD
	Chamaedorea *polychlada*	F	A	
	Chamaedorea sp. CR 466, CR 467	F	S	BD
	Geonoma *weberbaueri*	F	VA	BD
	Prestoea aff. *purpurea*	F	S	
Boraginaceae				
	Tournefortia *gigantifolia* Killip	F	VS	
Bromeliaceae				
	Ronnbergia aff. *deleani* L.B. Smith	F	VS	
Campanulaceae				
	Burmeistera aff. *longifolia* Gleason	F	S	
	Burmeistera *carnosa* Gleason	LD	A	
	Burmeistera sp.	LD-F	S	BD
	Burmeistera sp. nov. CR 543, CR 716, CR 734, CR 502	LD-F	A	BD
Clusiaceae				
	Clusia sect. Anandrogyne, "*A*. *multiflora* H.B.K.group"CR 796	LD-F	VS	BD
Cyclanthaceae				
	Asplundia sp.1	F	A	
	Asplundia *stenophylla* CR 553, CR 680, CR 579, CR 766	F	S	
	Spheraedenia sp.	F	S	

	CR 789			
	Spheraedenia steyermarkii	LD-F	A	BD
Ericaceae				
	Cavendishia engleriana Hoer.	F	S	BD
	Cavendishia tarapotana (Benth.) Meisner	G	VS	BD
	CR 666, CR 657, CR 590			
	Macleania stricta A.A. Smith	LD	VS	
	Psammisia aff. *debilis* Sleumer sp. nov.	LD	A	
	Psammisia cf. *dolichopoda* A.A. Smith	F	S	
	Psammisia cf. *ulbrichiana* Hoerold.	G	S	
	Psammisia ferruginea A.A. Smith	G	VS	
	Psammisia sodiroi Hoerold.	F	S	
Gesneriaceae				
	Alloplectus sp.	G	S	
	CR 475, CR 761			
	Alloplectus sp.1	F	VS	
	CR 790, CR 654			
	Alloplectus tenuis Benth.	G	S	
	Alloplectus tetragonus (Hanst.) Hanst.	G	S	
	Alloplectus teuscheri (Raymond) Wiehler	F	VA	
	Besleria solanoides	LD	VA	BD
	Besleria sp.	LD-G	S	
	CR 759			
	Columnea byrnsina (Wiehler) L.P. Kvist & L.E. Skog	LD	S	BD
	Columnea cinerea	LD	A	BD
	Columnea eburnea (Wiehler) L.P. Kvist & L.E. Skog	F	VS	
	Columnea eubracteata	LD	S	BD
	Columnea gigantifolia	F	S	BD
	Columnea minor	LD	S	
	Drymonia sp.	F	S	BD
	CR 559, CR 688, CR 540, CR 400			

	Drymonya warszewicziana Hanst.	G	S	
	Gasteranthus aff. *wendladianus* (Hanst.) Wiehler	LD-F	S	
	Unknown CR 582, CR 647, CR 541, CR 499	F	S	
Marcgraviaceae				
	Marcgravia eichleriana Wittmack	F	VS	BD
	Marcgraviastrum subssesilis (Benth) Bedell	F	VS	
Melastomataceae				
	Blakea cf. *stipulacea* Wurdack	G	S	BD
	Blakea punctulata (Triana) Wurdack	G	VS	
	Clidemia sp.1	LD-F	VA	BD
	Clidemia sp.2	F	S	BD
	Miconia aff. *neurotricha*	F	S	
	Miconia loreyoides Triana	LD	VS	BD
	Miconia pseudoradula Cogn. & Gleason ex Gleason	LD	VS	BD
	Miconia smaragdina Naudin	LD	VS	BD
	Miconia sp.5 CR 533, CR 745, CR 602	LD	VS	BD
	Miconia theaezans (Bonpl.) Cogn.	LD	VS	BD
	Ossaea micrantha (Sw.) Macf. ex Cogn.	F	VS	BD
	Topobea pittieri Cogn.	F	S	BD
	Topobea sp. CR 263	F	VS	
	Unknown CR 676, CR 415, CR 433	F	VS	
Meliaceae				
	Ruagea glabra	F	VS	

Monnimiaceae				
	Siparuna sp.	LD	S	
	CR 694			
Myrsinaceae				
	Cybianthus simplex (Hook.f.)Agost.	F	S	
Myrtaceae				
	Eugenia anastomosus DC	F	VS	
Onagraceae				
	Fuchsia macrostigma Bentham	LD	VS	
Rubiaceae				
	Faramea affinis	F-LD	VA	BD
	Faramea killipii Standl.	F	S	BD
	Palicourea gibbosa	F-LD	VA	BD
	Palicourea sp.1	LD	S	
	CR 461, CR 695			
	Palicourea sp.2	F	VS	
	CR 430			
	Psycothria aubletiana Steyerm.	F	VA	BD
	Psycothria hazenii Standl.	F	S	BD
	Psycothria panamensis Standl.	LD-F	S	BD
	Psycothria solitudinum Standl.	LD	S	
Solanaceae				
	Cestrum sp.	F	S	
	CR 485, CR 535, CR 779			
	Physalis sp.	G	S	
	Solanum evolulifolium	G	S	
	CR 487, CR 684		S	
	Solanum lepidotum	LD	S	BD
	CR 570, CR 711, CR 489, CR 799			
	Solanum sp.2	G	VS	

	CR 753, CR 627			
	Solanum sp.5	F	A	
	CR 483, CR 722, CR 794, CR 785			
	Solanum sp.7	G-LD	VA	
	CR 537, CR 735, CR 532?			
	Solanum sp.8	F	S	
	CR 486, CR 750, CR 762			
Zingiberaceae				
	Renealmia aff. *concinna* Standley sp. nov.	F	VS	
	CR 638			
New Edges				
Acanthaceae				
	Mendocia orbicularis Turrill	F	VS	
Araceae				
	Anthurium cf. *chamberlainii* Masters	F	ES	
	Anthurium sp. nov.	G	ES	
	CR 556			
	Philodendron oligospermum Engl	LD	VS	
	Stenospermatium longipetiolatum Engl.	LD	VS	BD
	Stenospermatium longispadix Croat	LD	VS	BD
	Stenospermatium sparrei Croat	LD	ES	
	Xanthosoma subandinum Schott	F	ES	
Araliaceae				
	Schefflera cf. *violacea* Cuatr.	F	ES	
Campanulaceae				
	Centropogon aff. *solanifolius* Benth	LD	ES	
Cyclanthaceae				
	Asplundia stenophylla	F	VS	
	Dicranopygium sp.	F	A	BD

	CR 552, CR 771, CR 551, CR 506		
Ericaceae			
	Psammisia montana Luteyn sp. nov.	F	VS
Gesneriaceae			
	Alloplectus bolivianus (Britton) Wiehler	F	VS
	Columnea cf. picta Karsten	G	ES
	Drymonia turrialvae Hanst.	G	VS
	Gasteranthus aff. oncogastrus (Hanst.)	G	S
	Gasteranthus oncogastrus (Hanst.) Wiehler	G	S
	Kohleria villosa (Fritsch) Weihler	G	ES
Heliconiaceae			
	Heliconia impudica Abalo & Morales	G	ES
Melastomataceae			
	Blakea cf. quadriflora Gleason	F	ES
	Miconia hymenanthera Triana		VS
Meliaceae			
	Unknown CR 751	F	ES
Phytolacaceae			
	Phytolacca rivinoides Kunth & Bouche	G	ES
Piperaceae			
	Piper gutierrezii T.&J.		ES
Rubiaceae			
	Palicourea sp.4 CR 592	G	ES
	Palicourea standleyana A.M. Taylor	G	S
	Psycothria allenii Standl.	F	ES
	Psycothria braulioi A.M. Taylor sp. nov.	G	ES

	CR 749, CR 637, CR 544			
	Psycothria dukei Dwyer	F	S	
Solanaceae				
	Solanum sp.3		ES	
	CR 754			
	Solanum sp.6	F	VS	
	CR 536, CR 658, CR 484			
	Unknown	LD	ES	
	CR 640, CR 661			
Unknown	CR 665	F	ES	
Unknown	CR 769	G	ES	
Old Edges				
Actinidaceae				
	Saurauia parviflora Tr. & Pl.	LD	ES	BD
Amaralidaceae				
	Bomarea pardina Herbert	LD	ES	
Clusiaceae				
	Clusia venusta Little	F	ES	
Ericaceae				
	Macleania bullata	LD	S	BD
	Sphyrospermum cordifoliium Bentham	F	ES	BD
Euphorbiaceae				
	Hyeronyma sp.	LD-F	ES	BD
	CR 706			
Gesneriaceae				

	Alloplectus schultzei Mansf.	F	ES	
Loranthaceae				
	Struthanthus aequatoris Kuijt	LD-F	ES	
Moraceae				
	Ficus cf. *apollinaris*	G	ES	
	Ficus garcia-barrigae	G	ES	
Myrsinaceae				
	Cybianthus sprucei (Hook.f.)Agos.	F	ES	
Rubiaceae				
	Hoffmania sp.	LD	ES	BD
Loranthaceae				
	Aetanthus sp.	F	ES	
Lauraceae				
	Unknown	F	ES	

APPENDIX B
BIRDS CAPTURED IN THE UNDERSTORY OF THE RESERVA NATURAL LA PLANADA

APPENDIX B
BIRDS CAPTURED IN THE UNDERSTORY OF THE RESERVA NATURAL LA PLANADA (JUNE 1992-AUGUST 1993)

Birds mist netted in the understory of the Reserva Natural La Planada. Abundance (AB): extremely sparse (ES), very sparse (VS), sparse (S), abundant (A), and very abundant (VS) Feeding guild (FG): carnivores (A), frugivores (F), insectivores (I), and nectarivores (N).

FAMILY	SPECIES	AB	FG	Mass (g)
Accipitridae	*Accipiter collaris*	VS	A	166.3
Columbidae	*Columba cayannensis*	VS	F	
Strigidae	*Glaucidium jardinii*	ES	A	75.0
	Otus columbianus	VS	A	165.0
Trochilidae	*Adelomyia melanogenys*	ES	N	5.2^2
	Aglaiocercus coelestis	VA	N	
	Amazilia franciae	ES	N	5.0^2
	Boissonneaua jardini	VS	N	9.8
	Chlorostilbon mellisugus	ES	N	4.0
	Coeligena torquata	VS	N	8.2
	Coeligena wilsoni	VA	N	7.1
	Colibri thalassinus	ES	N	
	Doryfera ludoviciae	ES	N	6.0
	Eutoxeres aquila	ES	N	9.5
	Haplophaedia lugens	VA	N	6.0

	Heliodoxa imperatrix	VS	N	8.2
	Lafresnaya lafresnayi	VS	N	5.0
	Ocreatus underwoodii	S	N	2.9
	Phaetornis syrmatophorus	VA	N	6.0
	Schistes geoffroyi	VS	N	4.0
	Urosticte benjamini	ES	N	4.4
Trogonidae				
	Trogon personatus	S	F	58.6
Capitonidae				
	Semnornis ramphastinus	VS	F	92.1
Ramphastidae				
	Andigena laminirostris	VS	F	349.5
Picidae				
	Campephilus pollens	ES	I	206.0
Dendrocolaptidae				
	Dendrocincla tyrannina	VS	I	53.4
	Glyphorynchus spirurus	VA	I	14.3
	Lepidocolaptes affinis	VS	I	29.0
	Xiphocolaptes promeropirhynchus	ES	I	161.0
Furnariidae				
	Anabacerthia variegaticeps	ES	I	25.0
	Cranioleuca erythrops?	ES	I	14.0
	Margarornis stellatus	S	I	20.7
	Premnoplex brunnescens	VA	I	15.9
	Premnornis guttuligera	VA	I	14.8
	Schizoeaca fuliginosa	ES	I	15.5
	Sclerurus mexicanus	S	I	22.3
	Syndactyla subalaris	A	I	32.9
	Thripadectes ignobilis	S	I	45.5
	Thripadectes virgaticeps	S	I	58.9
Formicariidae				

	Drymophila caudata	VS	I	10.5
	Formicarius rufipectus	VS	I	68.5
	Grallaricula flavirostris	1	I	20.4
	Thamnophilus unicolor	S	I	23.3
Cotingidae				
	Pachyramphus albogriseus	ES	F	16.1
	Pachyramphus versicolor	ES	F	15.0
	Pipreola riefferii	A	F	51.5
	Lipaugus cryptolophus	S	F	80.4
Pipridae				
	Allacotopterus deliciosus	A	F	12.4
	Masius chrysopterus	VA	F	11.5
Tyrannidae				
	Mionectes striaticollis	VA	F	13.8
	Myiobius barbatus	ES	I	12.0
	Myiophobus flavicans	A	I	12.9
	Myiotriccus ornatus	A	I	10.4
	Myiodynastes chrysocephalus	VS	I	38.8
	Ochtoeca cinnamomeiventris	VS	I	12.2
	Pogonotriccus ophtalmicus	VS	I	9.5
	Pseudotriccus pelzelni	VA	I	11.8
	Pseudotriccus ruficeps	ES	I	9.5
	Zimmerius viridiflavus	VS	F	10.2
Troglodytidae				
	Henicorhina leucophrys	VA	I	15.6
Turdidae				
	Catharus ustulatus	ES	F	29.5
	Entomodestes coracinus	VS	F	14.5
	Myadestes ralloides	VA	F	28.5
	Turdus serranus	ES	F	28.4[1]
Vireonidae				

	Vireo leucophrys	ES	I	22.0
Parulidae				
	Basileuterus coronatus	S	I	17.1
	Basileuterus tristriatus	VA	I	13.1
	Myioborus miniatus	VS	I	8.2
Thraupidae				
	Anisognathus flavinucha	VS	F	44.4
	Chlorochrysa phoenicotis	S	F	20.6
	Chlorospingus semifuscus	A	F	28.1
	Diglossa albilatera	S	N	9.9
	Diglossa indigotica	ES	N	12.0
	Euphonia xanthogaster	VA	F	13.6
	Iridosornis porphyrocephala	ES	F	26.0
	Tachyphonus luctuosus	ES	F	35.0
	Tangara arthus	S	F	20.8
	Tangara labradorides	VS	F	14.2
	Tangara nigroviridis	S	F	16.9
Catamblyrhynchidae				
	Catamblyrhynchus diadema	ES	I	18.0
Fringillidae				
	Amaurospiza concolor	VS	F	16.0
	Atlapetes brunneinucha	A	F	45.6

[1] Arango (1993); [2] Miller (1963)

LITERATURE CITED

Acevedo, C. I. 1987. Contribución al conocimiento de las relaciones entre colibrís y flores con observaciones de sus ciclos anuales en el bosque altoandino de Iguaque, Boyacá. Tesis, Departamento de Biología, Pontificia Universidad Javeriana, Bogotá, Colombia.

Ågren, J. 1988. Seed size and number in Rubus chamaemorus: beween-habitat variation, and effects of defoliation and supplemental pollination. Journal of Ecology **77**:1080-1092.

Ågren, J. 1989. Sexual differences in biomass and nutrient allocation in the dioecious Rubus chamaemorus. Ecology **69**:962-974.

Aizen, M. A. and P. Feinsinger. 1994. Forest fragmentation, pollination, and plant reproduction in a Chaco Dry Forest, Argentina. Ecology **75**:330-351.

Andrade, G. I., editor. 1993. Carpanta Selva Nublada y Páramo. Fundación Natura, Santa Fé de Bogotá, Colombia.

Andrade, G. I., H. Rubio-T. 1994. Sustainable use of the tropical rainforest: evidence from the avifauna in a shifting-cultivation habitat mosaic in the Colombian Amazon. Conservation Biology **8**:545-554.

Andrade, G. I., M. L. Rosas and A. Repizzo. 1993. Notas preliminares sobre la avifauna y la integridad biológica de Carpanta. Pages 207-228, *in* G. I. Andrade, editor. Carpanta Selva Nublada y Páramo. Fundación Natura, Santa Fé de Bogotá, Colombia.

Andrén, H. and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. Ecology **69**:54-547.

Arango, N. 1991. Depredación de nido y su relación con la fragmentación de habitat en un bosque nublado tropical. Tesis B.Sc., Departamento de Biología, Universidad del Valle, Cali, Colombia.

Arango, S. 1993. Morfología y comportamiento alimenticio de las aves frugívoras de Carpanta. Pages 127-140, *in* G.I.

Andrade, editor. Carpanta Selva Nublada y Páramo. Fundación Natura, Santa Fé de Bogotá, Colombia.

Arango, S. 1994. El papel de las aves dispersoras de semillas en la regeneración de pastizales en el Alto Quindío, Andes Centrales, Colombia. Fundación Herencia Verde, Cali, Colombia, *unpublished report*.

Arias, J. C. 1993. Polinización y biología reproductiva de Palicourea gibbosa Dwyer (Rubiaceae) en bosques de estados sucesionales diferentes. Tesis Biología, Universidad de Antioquia, Colombia.

Auchter, E. C., A. Lee Schrader, F. S. Lagasse, and W. W. Aldrich. 1926. The effect of shade on the growth, fruit bud formation and chemical composition of apple trees. Proceedings of the American Society for Horticultural Science **23**:368-382.

Auclair, A. N. and G. Cottam. 1971. Dynamics of black cherry (Prunus serotina Ehrh.) in southern Wisconsin oak forests. Ecological Monographs **41**:153-177.

Banguero, H. 1993. La población de Colombia 1938-2025. Una visión retrospectiva y prospectiva para el país, los departamentos y sus municipios. Colección de Edición Previa, Editorial Universidad del Valle, Cali, Colombia.

Beltrán, W. 1991. Historia natural de Andigena laminirostris (Aves: Ramphastidae). Informe Final, Fundación para la Promoción de la Investigación y la Tecnología, Banco de la República, Bogotá, Colombia.

Bierregaard, R. O. 1990. Avian communities in the understory of Amazonia forest fragments. Pages 333-343, *in* A. Keast, editor. Biogeography and Ecology of Forest Bird Communities. SPB Academic Publishing bv, Hague, The Netherlands.

Bierregaard, R. O., Jr. and T. E. Lovejoy. 1989. Effects of forest fragmentation on amazonian understory bid communities. Acta Amazonica **19**:215-241.

Blake, J. G. and W. G. Hoppes. 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. Auk **103**:328-340.

Blake, J. G. and B. A. Loiselle. 1991. Variation in resource abundance affects capture rates of birds in three lowland habitats in Costa Rica. Auk **108**:114-130.

Blake, J. G., B. A. Loiselle, T. C. Moermond, D. J. Levey, and J.S. Denslow. 1990. Quantifying abundance of fruits for birds in tropical habitats. Studies in Avian Biology **13**:73-79.

Blanchard, J. D. 1992. Light, vegetation structure, and fruit production on edges of clearcut sand pine scrub in Ocala National Forest, Florida. M.Sc. Thesis, University of Florida, Gainesville, FL.

Brittingahm, M. C. and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? BioScience **33**:31-35.

Brokaw, N. V. L. 1982. The definition of treefall gap and its effect on measures of forest dynamics. Biotropica **11**:158-160.

Brown, J. H. 1995. Macroecology. The University of Chicago Press, Chicago, IL.

Brown, N. 1993. The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rain forest. Journal of Tropical Ecology **9**:133-168.

Burkey, T. V. 1993. Edge effects in seed and egg predation at two neotropical rainforest sites. Biological Conservation **66**:139-143.

Bush, B. M. 1994. Amazonian speciation: a necessary complex model. Journal of Biogeography **21**:5-17.

Cavelier, J. and A. Etter. Deforestation of mountain forest in Colombia as a result of illegal plantation of opium (Papaver somniferum) in Neotropical Mountain Forest. Proceedings of the Neotropical Mountain Forest Biodiverstiy and Conservation Symposium, New York Botanical Garden, New York, August 1992, *in press*.

Chaikiattiyos, S., C. M. Menzel, and T. S. Rasmussen. 1994. Floral induction in tropical fruit trees: Effects of temperature and water supply. Journal of Horticultural Science **69**:397-415.

Chapman, F. M. 1917. The distribution of bird life in Colombia. Bulletin of the American Museum of Natural History **33**:167-192.

Chason, J. F., D. D. Baldocchi and M. A. Huston. 1991. A comparison of direct and indirect methods for estimating forest canopy leaf area. Agricultural and Forest Meteorology **57**:107-128.

Chen, J., J. F. Franklin, and T. A. Spies. 1992. Vegetation responses to edge environments in Old-growth Douglas-Fir forests. Ecological Applications **2**:387-396.

Clark, D. A. and D. B. Clark. 1987. Temporal and environmental patterns of reproduction in Zamia skinneri, a tropical rain forest cycad. Journal of Ecology **75**:135-149.

Clark, W. C., D. D. Jones, and C. S. Holling. 1979. Lessons for ecological policy design: A case study of ecosystems management. Ecological Modelling **7**:1-53.

Compton, S. G., S. J. Ross, and I. W. R. Thornton. 1994. Pollinator limitation of fig tree reproduction on the island of Anak Krakatau (Indonesia). Biotropica **26**:180-186.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science **199**:1302-1309.

Corredor, G. L. 1989. Estudio comparataivo entre la avifauna de un bosque natural y un cafetal tradicional en el Quindio. Trabajo de Grado, Departamento de Biología, Universidad del Valle, Cali, Colombia.

Correll, D. L. 1991. Human impact on the functioning of landscape boundaries. Pages 90-109, *in* M. J. Holland, P. G. Risser, and R. J. Naiman, editors. Ecotones: The Role of Landscape Boundaries in the Management and Restoration of Changing Environments. Chapman Hall, New York, USA.

Crist, T. O. and J. A. MacMahon. 1991. Individual foraging components of harvester ants: movement patterns and seed patch fidelity. Insect Socieux **38**:379-396.

Crist, T. O., D. S. Guertin, J. A. Wiens, and B. T. Milne. 1992. Animal movement in heterogeneous landscapes: an experiment with Eleodes beetles in shortgrass prairie. Functional Ecology **6**:536-544.

Cronquist, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia University Press, New York, NY.

Cuadros, T. 1988. Aspectos ecológicos de la comunidad de aves en un bosque nativo en la Cordillera central en Antioquia, Colombia. Hornero **13**:8-20.

Cuatrecasas, J. 1958. Aspectos de la vegetación natural. Revista de la Academia Colombiana de Ciencias Exactas Físicas y Naturales **10**:221-264.

Dalling, J. W. and E. V. J. Tanner. 1995. An experimental study of regeneration on landslides in montane rain forest in Jamaica. Journal of Ecology **83**:55-64.

De las Salas, G. and M. Ballesteros. 1986. Tipos de comunidades forestales de la Reserva Natural La Planada, Nariño, Colombia. Informe Final FES, Cali, Colombia

DeGraaf, R. M. 1992. Effects of even-aged management on forest birds at northern hardwood stand interfaces. Forest Ecology and Management **46**:95-110.

del Hoyo, J., A. Elliott, and I. Sargatal, editors. 1992. Handbook of the Birds of the World. Lynx Ediciones, Barcelona, España.

Denslow, J. S. and G. S. Hartshorn. 1994. Tree-fall gap environments and forest dynamic processes. Pages 120-127, *in* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, editors. La Selva: Ecology and Natural History of a Neotropical Rain Forest. The University of Chicago Press, Chicago, IL.

Denslow, J. S. and A. E. Gomez-Díaz. 1990. Seed rain to treefall gaps in a neotropical forest. Canadian Journal of Forest Researach **20**:642-648.

Didham, R. The influence of edge effects and forest fragmentation on leaf litter invertebrates in central Amazonia. *in* W.F. Laurance and R.O. Bierregaard, Jr., editors. Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities, *in press*.

Draiijers, G. P. J., W. P. M. F. Ivens, and W. Bleuten. 1988. Atmospheric deposition in forest edges measured by monitoring canopy throughfall. Water, Air, and Soil Pollution **42**:129-136.

Duellman, W. E. 1979. The herpetofauna of the Andes: patterns of distribution, origin, differentiation, and present communities. Pages 371-45 *in* W.E. Duellman, editors. The South American Herpetofauna: Its Origin, Evolution, and Dispersal. Museum of Natural History, Monograph **7**, University of Kansas, Lawrence, Kansas.

Dunning, J. B., Jr. 1993. Handbook of Avian Body Masses. CRC Press, Boca Raton, FL.

Dwyer, J. D. 1980. Family 179. Rubiaceae, Part II. Annals of the Missourit Botanical Garden **67**:257-522.

Ellison, A. M., J. S. Denslow, B. A. Loiselle, and D. Brenés. 1993. Seed and seedling ecology of neotropaical Melastomataceae. Ecology **74**:1733-1749.

Escobar, F. 1994. Excremento, coprófagos y deforestación en bosques de montaña al suroccidente de Colombia. Tesis, Universidad del Valle, Cali, Colombia.

Espinal, L. S., J. Tosi Jr., E. Montenegro, G. Toro and D. Díaz. 1977. Zonas de vida o formaciones vegetales de Colombia. Instituto Geográfico Agustín Codazzi, Bogotá, Colombia.

Esseen, P. A. 1994. Tree mortality patterns after experimental fragmentation of an old-growth conifer forest. Biological Conservation **68**:19-29.

Estrada, A., R. Coates-Estrada, D. Meritt, S. Montiel, and D. Curiel. 1993. Patterns of frugivore species richness and abundance in forest islands and in agricultural habitats at Los Tuxtlas, Mexico. Vegetatio **107/108**:245-257.

Ewel, J. and A. Madríz. 1968. Zonas de vida de Venezuela. Memoria Explicativa sobre el Mapa Ecológico. Editorial Sucre, Venezuela.

Feinsinger, P., J. H. Beach, Y. B. Linhart, W. H. Busby, and K. G. Murray. 1987. Disturbance, pollinator predictability, and pollination success among Costa Rican Cloud forest plants. Ecology **68**:1294-1305.

Feinsinger, P., H. M. Tiebout III, and B. E. Young. 1991. Do tropical bird-pollinated plants exhibit densigy-dependent interactions? Field experiments. Ecology **72**:1953-1963.

Fitzpatrick, J. W. 1980. Foraging behavior of neotropical tyrant flycatchers. Condor **82**:43-57.

Fjeldså, J. and N. Krabe. 1990. Birds of the high Andes. Zoological Museum, University of Copenhagen and Apollo Books, Svendborg, Denmark.

Fleming, T. H. 1988. The Short-tailed Fruit Bat: A Study in Plant-Animal Interactions. Wildlife Behavior and Ecology Series, Chicago Press, Chicago, IL.

Gagnon, J., K. A. Haycock, J. R. Roth, D. S. Feldman, Jr., W. F. Finzer, R. Hofman, and J. Simpson. 1989. SuperANOVA. Accesible General Linear Modeling. Abacus Concepts, Berkely, CA.

Garwood, N., D. P. Janos, and N. Brokaw. 1979. Earthquake-caused landslides: a major disturbance to tropical forests. Science **205**:997-999.

Gaston, K. J. and T. M. Blackburn. 1995. Birds, body size and the threat of extinction. Philosophical Transactions of the Royal Society of London B **347**:205-212.

Gates, J. E. and L. W. Gysel. 1978. Avian nest dipsersion and fledgling success in field-forest ecotones. Ecology **59**:871-883.

Geiger, R. 1965. The Climate Near the Ground. Harvard University Press, Cambridge, MA.

Gentry, A. H. 1983. Dispersal ecology and diversity in neotropical forest communities. Sonderband naturwisseschaften Ver. Hamburg **7**:303-314.

Gentry, A. H. 1986. Endemism in tropical versus temperate plant communities. Pages 153-181, *in* M. Soulé (editor). Conservation Biology: The Science of Scaracity and Diversity. Sunderland, MA.

Gentry, A. H. 1988. Changes in plant communty diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden **75**:1-34.

Gentry, A. H. 1992a. Diversity and composition of Andean forests of Peru and adjacent countries: implications for their conservation. Memorias del Museo de Historia Natural U.N.M.S.M. (Lima) **21**:11-29.

Gentry, A. H. 1992b. Tropical forest biodiversity: distributional patterns and their conservational significances. Oikos **63**:19-28.

Gentry, A. H. and L. H. Emmons. 1987. Geographical variation in fertility, phenology, and composition of understory neotropical forests. Biotropica **19**:216-227.

George, A. P., R. J. Nissen, and C. Howitt. 1990. Effects of environmental variables and cropping on leaf conductance of custard apple (Annona cherimola x Annona squamosa) 'African Pride'. Scientia Horticulturae **45**:137-147.

Gibbs, J. P. 1991. Avian est predation in tropical wet forest: an experimental study. Oikos 60:155-161.

Girden, E. R. 1992. ANOVA: Repeated Measures. Sage University Paper Series on Quantitative Applications in the Social Sciences, 07-84, Newbury Park, CA.

Gómez, M. E. and C. Palau. 1994. El campesino de San Isidro, Nariño: Condiciones de vida y participación en programas de desarrollo en la zona de influencia de la Reserva Natural La Planada. Tesis Pregrado, Universidad del Valle, Cali, Colombia.

Goodwin, D. 1976. Crows of the World. Comstock Publishers Associate, Ithaca, New York, USA.

Gosz, J. R. 1991. Fundamental ecological characteristics of landscape boundaries. Pages 8-30 *in* M. J. Holland, P. G. Risser, and R. J. Naiman, editors. Ecotones: The Role of Landscape Boundaries in the Management and Restoration of Changing Environments. Chapman Hall, New York, USA.

Grubb, P. J. 1977. Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. Annual Review of Ecology and Systematics **8**:83-107.

Guariguata, M. R. Landslide disturbance and forest regeneration in the upper Luquillo mountains of Puerto Rico. Journal of Ecology **78**:814-832.

Guimarães, I. C., C. Uhl, and D. Nepstad. 1994. The role of the shrub Cordia multispicata Cham as a succcession facilitator in an abandoned pasture, Paragominas, Amazônia. Vegetatio **115**:91-99.

Gunderson, L. H. 1992. Spatial and temporal dynamics in the Everglades ecosystem with implications for water deliveries to Everglades National Park. Ph.D. Dissertation, University of Florida, Gainesville, FL.

Haffer, J. 1969. Speciation in Amazonian birds. Science **165**:131-137.

Halls, L. K. 1973. Flowering and fruiting of Southern browse species. U.S. Forest Service Research Paper SO-90:1-10.

Hannan, N. P. and A. Bégué. 1995. A method to estimate instantaneous and daily intercepted photosynthetically active radiation using a hemispherical sensor. Agricultural and forest Meteorology **74**:155-168.

Hansen, A. J., D. L. Urban, and B. Marks. 1992. Avian community dynamics: the interplay of landscape trajectories and species life histories. Pages 170-195, *in* A.J. Hansen and F. di Castri, editors. Landscape

Boundaries: Consequences for Biotic Diversity and Ecological Flows. Springer-Verlag, New York, NY.

Hansson, L. 1983. Bird numbers across edges between mature conifer forest and clear cuts in Central Sweden. Ornis Scandinavica **14**:97-103.

Harper, J. L. 1994. Population Biology of Plants. Academic Press, San Diego, Californa, USA.

Harris, G. P. 1980. Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, models, and management. Canadian Journal of Fisheries and Aquaculture **37**:877-900.

Harris, L. D. 1984. The Fragmented Forest. University of Chicago Press, Chicago, IL.

Haslett, J. A. 1994. Community structure and the fractal dimensions of mountain habitats. Journal of Theoretical Biology **167**:407-411.

Heideman, P. D. 1989. Temporal and spatial variation in the phenology of flowering and fruiting in a tropical rainforest. Journal of Ecology **77**:1059-1079.

Henderson, A., S. P. Churchill and J. Luteyn. 1991. Neotropical plant diversity. Nature **351**:21-22.

Hilty, S. L. 1980. Flowering and fruiting periodicity in a premontane rain forest in Pacific Colombia. Biotropica **12**:292-306.

Hilty, S. L. and W. L. Brown. 1986. A Guide to the Birds of Colombia. Princeton University Press, Princeton, NJ.

Holdridge, L. R. 1967. Life Zone Ecology. Tropical Science Center, San José, Costa Rica.

Holdridge, L. R., W. C. Grenke, W. H. Hateway, T. Liang, and J. A. Tosi, Jr. 1971. Forest Environments in Tropical Life Zones, A Pilot Study. Pergamon Press, Oxford, UK.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics **4**:1-23.

Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs **62**:447-502.

Holling, C. S., G. Peterson, P. Marples, J. Sendzimir, K. Redford, L. Gunderson, and D. Lambert. 1995. Self-organization in ecosystems: lump geometries, periodicities, and morphologies. *in* B. H. Walker and W. L. Steffen, editors. Global Change and Terrestrial Ecosystems. Cambridge University Press, Cambridge, Massachusetts, USA, *in press*.

Holloway, J. D., A. H. Kirk-Spriggs and C. von Khen. 1992. The response of some rain forest insect groups to logging and conversion to plantation. Philosophical Transactions of the Royal Society of London B **335**:425:436.

Hooghiemstra, H. 1984. Vegetational and climatic history of the high plain of Bogota, Colombia: A continuous record of the last 3.5 million years. Dissertationes Botanicae **79**. Cramer, Vaduz.

Hubbell, S. G. and R. B. Foster. 1987. Biology, chance, and history and the structure of tropical rain forest tree communities. Pages 314-329, *in* J. Diamond and T. J. Case, editors. Community Ecology. Harper and Row, New York, NY.

Hughes, L., M. Dunlop, K. French, M. R. Leishman, B. Rice, L. Rodgerson, and M. Westoby. Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. Journal of Ecology **82**:933-950.

Irving, E. M. 1975. Structural evolution of the northernmost Andes, Colombia. U.S. Geological Survey Professional Paper 846, Washington, DC, USA.

Isler, M. L. and P. R. Isler. 1987. The Tanagers: Natural History, Distribution and Identification. Smithsonian Institution Press, Washington, DC, USA.

Jackson, J. E. and J. W. Palmer. 1977. Effects of shade on the growth and cropping of apple trees. II. Effects on components of yield. Journal of Horticultural Science **52**:253-266.

Janzen, D. H. 1983. No park is an island: Increase in interference from outside as park size decreases. Oikos **41**:402-410.

Johnels, S. A. and T. C. Cuadros. 1986. Species composition and abundance of bird fauna in a disturbed forest in the Central Andes of Colombia. Hornero **12**:235-241.

Johns, A. D. 1992. Vertebrate responses to selective logging: implications for the design of logging systems. Philosophical Transactions of the Royal Society of London B **335**:437-442.

Johnson, A. R., B. T. Milne, and J. A. Wiens. 1992. Diffusion in fractal landscapes: simulations and experimental studies of Tenebronid beetle movements. Ecology **73**:1968-1983.

Kapos, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. Journal of Tropical Ecology **5**:173-185.

Kapos, V., E. Wandelli, J. L. Camargo, and G. Ganade. Edge-related changes in environment and plant responses due to forest fragmentation in Central Amazonia. *in* W. F. Laurance and R. O. Bierregaard, Jr., editors. Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities, *in press*.

Kapos, V., G. Ganade, E. Matsui, and R. L. Victoria. 1993. $\partial^{13}C$ as an indicator of edge effects in tropical rainforest reserves. Journal of Ecology **81**:425-432.

Karr, J. R. 1971. Structure of avian communities in selected Panama and Illinois habitats. Ecological Monographs **41**:207-233.

Karr, J. R. 1981a. Surveying birds in the tropics. Studies in Avian Biology **6**:548-553.

Karr, J. R. 1981b. Surveying birds with mist nets. Studies in Avian Biology **6**:62-67.

Karr, J. R. and R. R. Roth. 1971. Vegetation structure and avian diversity in several new world areas. American Naturalist **105**:423-435.

Kattan, G. 1992. Rarity and vulnerability: The Birds of the Cordillera Central of Colombia. Conservation Biology **6**:64-70.

Kattan, G., C. Restrepo, and M. Giraldo. 1984. Estructura de un bosque de niebla en la Cordillera Occidental, Valle del Cauca, Colombia. Cespedesia **13**:23-43.

Kattan, G. H., H. Alvarez-L. and M. Giraldo. 1994. Forest fragmentation and bird extinctions: San Antonio eighty years later. Conservation Biology **8**:138-146.

Kellman, M. and M. Kading. 1992. Faciliation of tree establishment in a sand dune succession. Journal of Vegetation Science **3**:679-688.

King, D. A. 1991. Allometry of saplings and understory trees of a Panamanian forest. Oecologia **51**:351-356.

Klein, B. C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in Central Amazonia. Ecology **70**:1715-1725.

Kroodsma, R. L. 1984. Effect of edge on breeding forest bird species. Wilson Bulletin **96**:426-436.

Kruess, A. and T. Tscharntke. 1994. Habitat fragmentation, species loss, and biological control. Science **264**:1581-1584.

Kuitunen, M. and M. Mäkinen. 1993. An experiment on nest site choice of the Common Treecreeper in fragmented boreal forest. Ornis Fennica **70**:163-167.

Lambert, F. R. 1992. The consequences of selective logging for Bornean lowland forest birds. Philosophical Transactions of the Royal Society of London B **335**:443-457.

Laurance, W. F. 1990. Comparative responses of five arboreal marsupials to tropical forest fragmentation. Journal of Mammalogy **71**:641-653.

Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conservation Biology **5**:79-89.

Laurance, W. F. 1993. Avian nest predation in modified and natural habitats in tropical Queensland: an experimental study. Wildlife Research **20**:711-723.

Laurance, W. F. 1994. Rainforest fragmentation and the structure of small mammal communities in tropical Queensland. Biological Conservation **69**:23-32.

Lawton, J. H., S. Nee, A. J. Letcher, and P. H Harvey. 1994. Animal distributions: patterns and processes. Pages 41-58 *in* P. J. Edwards, R. M. May, and N. R. Webb, editors. Large-scale Ecology and Conservation Biology. Blackwell Scientific Publications, Oxford, UK.

Lawton, R. and V. Dryer. 1980. The vegetation of the Monteverde Cloud Forest Reserve. Brenesia **18**:101-116.

Lawton, R. O. and F. E. Putz. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. Ecology **69**:764-777.

Leigh, E. G., Jr. 1975. Structure and climate in tropical rain forest. Annual Review of Ecology and Systematics. **6**:67-86.

Lescourret, F. and M. Genard. 1994. Habitat, landscape and bird composition in mountain forest fragments. Journal of Environmental Management **40**:317-328.

Levey, D. J. 1986. The role of seed size and bird species on seed deposition patterns, Pages 147-158, *in* A. Estrada and T.H. Fleming, editors. Frugivores and Seed Dispersal. Junk, Dordrecht, The Netherlands.

Levey, D. J. 1987. Seed size and fruit-handling techniques of avian frugivores. American Naturalist **129**:471-485.

Levey, D. J. 1988a. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. Ecological Monographs **58**:251-269.

Levey, D. J. 1988b. Tropical wet forest treefall gaps and distributions of understory birds and plants. Ecology **69**:1076-1089.

Levey, D. J. 1990. Habitat-dependent fruiting behaviour of an understorey tree, Miconia centrodesma, and tropical treefall gaps as keystone habitats for frugivores in Costa Rica. Journal of Tropical Ecology **6**:409-420.

Li-Cor, Inc. 1992. LAI-2000 Plant Canopy Analyzer Operating Manual. Li-Cor, Inc., Lincoln, NB.

Lipsey, M. W. 1990. Design Sensitivity: Statistical Power for Experimental Research. SAGE Publications, Inc., Newbury Park, California, USA.

Loiselle, B. A. and J. G. Blake. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology **72**:180-193.

Loiselle, B. A. and J. G. Blake. 1993. Spatial distribution of understory fruit-eating birds and fruiting plants in a neotropical lowland wet forest. Vegetatio **107/108**:177-189.

Lopez de Casenave, J., J. P. Pelotto, S. Caziani, M. Mermiz, and J. Protomastro. Edge effects in avian assemblages of a Chaco semiarid forest, Argentina. *Unpublished manuscript*.

Lovejoy, T. E., R. O. Bierregaard, A. B. Rylands, J. R. Malcolm, C. E. Quinetela, L. H. Harper, K. S. Browns, A. H. Powell, G. V. N. Powell, H. O. R. Schubart, and M. B. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257-285 *in* M. E. Soulé, editor. Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, Massachusetts, USA.

Loye, J. and S. Carroll. 1995. Birds, bugs and blood: avian parasitism and conservation. TREE **10**:232-235.

Lozano, I. E. 1993. Diversidad y organización en gremios de la comunidad de aves del sotobosque de bosque primario y vegetación secundaria. Pages 141-164, *in* G.I. Andrade, editor. Carpanta Selva Nublada y Páramo. Fundación Natura, Colombia.

Lugo, A. E. and J. L. Frangi. 1993. Fruit-fall in the Luquillo Experimental Forest, Puerto Rico. Biotropica **25**:73-84.

Lynam, A. J. Processes of local extinction of small mammals in a recently fragmented tropical monsoon forest in Thailand. *in* W.F. Laurance and R.O. Bierregaard, Jr., editors. Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities, *in press*.

Lynch, J. F. 1989. Distribution of overwintering nearctic migrants in the Yucatan Peninsula, I: General patterns of occurrence. Condor **91**:515-544.

MacDougall, A. and M. Kellman. 1992. The understory light regime and patterns of tree seedlings in tropical riparian forest patches. Journal of Biogeography **19**:667-675.

Malcolm, J. R. 1991. The small mammals of Amazonian Forest fragments: Pattern and process. Ph.D. Dissertation, University of Florida, Gainesville, FL.

Malcolm, J. R. 1994. Edge effects in Central Amazonian forest fragments. Ecology **75**:2438-2445.

Manly, B. F. 1992. The Design and Analysis of Research Studies. Cambridge University Press, Cambridge, UK.

Margalef, R. 1968. Perspectives in Ecological Theory. The University of Chicago Press, Chicago, IL.

Marshall, C. and J. Grace, editors. 1992. Fruit and Seed Production: Aspects of Development, environmental physiology and ecology. Cambridge University Press, Cambridge, UK.

Martin, T. E. 1985. Selection of second-growth woodlands by frugivorous migrating birds in Panama: an effect of fruit size and plant density? Journal of Tropical Ecology **1**:157-170.

Martínez-Ramos, M. and A. Soto-Castro. 1993. Seed rain and advanced regeneration in a tropical rain forest. Vegetatio **107/108**:299-318.

Mathai, C. K. and K. S. K. Sastry. 1988. Productivity of black pepper vines (Piper nigrum L.) as influences by the light availability during pre-flowering stage. Comparative Physiological Ecology **13**:97-102.

Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the Eastern United States. Biological Conservation **66**:185-194.

May, P. and A. J. Antcliff. 1963. The effect of shading on fruitfulness and yield in the sultana. Journal of Horticultural Science **38**:85-94.

McDiarmid, R. W., R. E. Ricklefs, and M. S. Foster. 1977. Dispersal of Stemmadenia donnellii-smithii (Apocynaceae) by birds. Biotropica **9**:9-25.

Mejía, J., H. Meyer, A. Campos, A. Gallego, and A. Velásquez. 1994. El terremoto de Paez, anatomía de un sismo, Parte I: generalidades y movimientos fuertes. Revista de la Asociación de Ingenieros del Valle (472):14-15.

Miller, A. H. 1963. Seasonal activity and ecology of the avifauna of an american equatorial cloud forest. University of California Publications in Zoology **66**:1-78.

Moermond, T. C. and J. S. Denslow. 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. Neotropical Monographs **36**:865-897.

Møller, A. P. 1989. Nest site selection across field-woodland ecotones: the effect of nest predation. Oikos **56**:240-246.

Mondragón, M. L. 1989. Estructura de la comunidad aviaria en bosques de coníferas y en bosques aledaños de vegetación nativa. Trabajo de Grado, Departamento de Biología, Universidad del Valle, Cali, Colombia.

Munves, J. 1975. Birds of highland clearing in Cundinamarca, Colombia. Auk **92**:307-321.

Murcia, C. 1993. Edge Effects on the Pollination of Tropical Cloud Forest Plants. Ph.D. Dissertation, University of Florida, Gainesville, FL.

Murray, K. G. 1987. Selection for optimal fruit-crop size in bird-dispersed plants. American Naturalist **129**:18-31.

Murray, K. G. 1988. Avian seed dispersal of three neotropical gap-dependent plants. Ecological Monographs **58**:271-298.

Naranjo, L. G. 1994. Composición y estructura de la avifauna del Parque Regional Natural Ucumarí. Pages 305-328 *in* J.O. Rangel, editors. Ucumarí: Un caso típico de la diversidad biótica Andina, Corporación Autónoma Regional de Risaralda, Colombia.

Newmark, W.D. 1991. Tropical forest fragmentation and the local extinction of understory birds in the eastern Usambara mountains, Tanzania. Conservation Biology **5**:67-78.

Noble, I. A. 1993. A model of the responses of ecotones to climate change. Ecological Monographs **3**:396-403.

Norman, J. M. and G. S. Campbell. 1991. Canopy structure, Pages 301-326, *in* R. W. Pearcy, J. Ehleringer, H. A. Mooney, and P. W. Rundel,editors. Plant Physiological Ecology. Chapman and Hall, London, UK.

Noss, R. F. 1991. Effects of edge and internal patchiness on avian habitat use in an Old-Growth Florida Hammock. Natural Areas Journal **11**:34-47.

Orejuela, J. E. 1987. La Reserva Natural La Planada y la biogeografía andina. Humboldtia **1**:117-148.

Orejuela, J. E. and G. Cantillo, compilers. 1980. Aves de la Reserva Natural La Planada. Programa Alegría de Enseñar, Fundación para la Educación Superior-FES, Cali, Colombia.

Orejuela, J. E., R. S. Raitt and H. Alvarez. 1979. Relaciones ecológicas de las aves en la Reserva Forestal de Yotoco, Valle del Cauca. Cespedesia **29-30**:7-28.

Osunkoya, O., J. E. Ash, M. S. Hopkins, and A. W. Graham. 1994. Influence of seed size and seedling ecological attributes on shade-tolerance of rain-forest tree species in northern Queensland. Journal of Ecology **82**:149-163.

Pacheco, S., N. Florencio da Silva, R. Ribon, J. E. Simon and R. Torres. 1994. Efeito do manejo do cerrado sobre as populações de algus Tinamidae em Tres Marias, Estado de Minas Gerais. Revista Brasilera Biologia **54**:435-441.

Pimm, S. L. and A. M. Sugden. 1994. Tropical diversity and global change. Science **263**:933-934.

Piñero, D. and J. Sarukhan. 1982. Reproductive behaviour and its individual variability in a tropical palm, Astrocaryum mexicanum. Journal of Ecology **70**:461-472.

Potvin, C. 1993. Experiments in controlled environments. Pages 46-68, *in* S.M. Scheiner and J. Gurevitch, editors. Design and Analysis of Ecological Experiments, Chapman Hall, New York, NY.

Poulin, B., G. Lefebvre, and. R. McNeil. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. Ecology **73**:2295-2309.

Quintela, C. 1986. Forest fragmentation and differential use of natural and man-made edges by understory birds in Central Amazonia. M.Sc. Thesis, University of Chicago, Chicago, IL.

Rangel, J. O., editor. 1994. Ucumarí: Un caso típico de la diversidad biótica Andina, Corporación Autónoma Regional de Risaralda, Colombia.

Ranney, J. W., M. C. Bruner, and J. B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. Pages 67-95, *in* R. L. Burguess and D. M. Sharpe, editors. Forest Island Dynamics in Man-Dominated Landscapes. Springer-Verlag, New York, NY.

Remsen, J.V., Jr. 1994. Use and misuse of bird lists in community ecology and conservation. Auk **111**:225-227.

Remsen, J. V., Jr. and T. A. Parker. 1983. Contribution of river-created habitats to bird species richness in Amazonia. Biotropica **15**:223-231.

Renjifo, L. M. 1988. Composición y estructura de la comunidad aviaria de bosque andino primario y secundario en la Reserva del Alto Quindío Acaime, Colombia. Tesis, Departamento de Biología, Pontificia Universidad Javeriana, Santa Fé de Bogotá, Colombia.

Renjifo, L. M., G. P. Servat, J. M. Goerck, B. A. Loiselle and J. G. Blake. Patterns of species composition and endemism in the northern Neotropics: a case for conservation of montane avifaunas. *in* J. V. Remsen, editor. Natural History and Conservation of Neotropical Birds, Ted Parker Memorial Volume, Ornithological Monographs, *in press*.

Restrepo, C. 1990. Ecology and cooperative breeding in a frugivorous bird, Semnornis ramphastinus. M.Sc. Thesis, University of Florida, Gainesville, FL.

Ridgely, R. S. and G. Tudor. 1989. The birds of South America. V1. The Oscine Passerines. University of Texas Press, Austin, TX.

Ridgely, R. S. and G. Tudor. 1994. The birds of South America. V 2. The Suboscine Passerines. University of Texas Press, Austin, TX.

Ridgely, R. S. and S. J. C. Gaulin. 1980. The birds of finca Merenberg, Huila department, Colombia. Condor **82**:379-391.

Romano, G. B. 1990. Invasibility of a Mixed Hardwood Forest by Eupatorium capillifolium and E. compositifolium. M.Sc. Thesis, Universtiy of Florida, Gainesville, FL.

Rosas, M. L. 1986. Estudio de la estructura de la comunidad de frugívoros en sotobosques del Cañon de Mamarramos en el Santuario de Fauna y Flora de Iguaque, Boyacá.Tesis, Departamento de Biología, Pontificia Universidad Javeriana, Santa Fé de Bogotá, Colombia.

Ryszkowski, L. 1992. Energy and material flows across boundaries in agricultural landscapes. Pages 270-284 *in* A.J. Hansen and F. di Castri, editors. Landscapes Boundaries: Consequences for Biotic Diversity and Ecological Flows. Springer-Verlag, New York, NY.

Salisbury, E. 1974. Seed size and mass in relation to environment. Proceedings of the Royal Society, London B **186**:83-88.

Salo, J., R. Kallioloa, R. Häkkinen, Y. Mäkinen, P. Niemelä, M. Puhakka, and P. D. Coley. 1986. River dynamics and the diversity of Amazon lowland forest. Nature **322**:254-258.

Samper, C. 1992. Natural disturbance and plant establishment in an Andean cloud forest. Ph.D. Dissertation, University of Harvard, Cambridge, MA.

Scheiner, S. M. 1993. Introduction: Theories, hypotheses, and statistics. Pages 1-13, *in* S. M. Scheiner and J. Gurevitch, editors. Design and Analysis of Ecological Experiments, Chapman Hall, New York, NY.

Schupp, E. W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. Oikos **51**:71-78.

Schupp, E. W. and E. J. Frost. 1989. Differential predation o Welfia georgii seeds in treefall gaps and the forest understory. Biotropica **21**:200-203.

Schupp, E. W., H. F. Howe, C. K. Augspurger, and D. J. Levey. 1989. Arrival and survival in tropical treefall gaps. Ecology **30**:562-564.

Seghieri, J., Ch. Floret, and R. Pontanier. 1995. Plant phenology in relation to water availability: herbaceous and woody species in the savannas of northern Cameroon. Journal of Tropical Ecology **11**:237-254.

Seizer, N. G. 1992. The impact of edge formation on regeneration and litterfall in a tropical rain forest fragment in Amazonia. Ph.D. Dissertation, University of Cambridge, Cambridge, UK.

Shoji, S., M. Nanzyo, and R. A. Dahlgren. 1993. Volcanic ash soils: Development, properties, and utilization. Developments in Soil Science 21. Elsevier Science Publishers B.V., Amsterdam, The Netherlands.

Siegel, S. and N. J. Castellan. 1988. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill Book Company, New York, NY.

Silverman, B. W. 1986. Density Estimation for Statistics and Data Analysis. Monographs on Statistics and Applied Probability 26, Chapman Hall, London, UK.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry. Freeman, New York, NY.

Sork, V. L. 1983. Distribution of pignut hickory (Carya glabra) along a forest to edge transect, and factors affecting seedling recruitment. Bulletin Torrey Botanical Club **110**:494-506.

Stephenson, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. Annual Review of Ecology and Systematics **12**:253-279.

Stephenson, A. G. 1992. The regulation of maternal investment in plants. Pages 151-172, *in* C. Marshall and J. Grace, editors. Fruit and Seed Production: Aspects of Development, Environmental Physiology and Ecology. Cambridge University Press, Cambridge, UK.

Stiles, F. G. 1985. On the role of birds in the dynamics of neotropical forests. ICBP Technical Publication **4**:49-59.

Stiles, F. G. and A. Skutch. 1989. A Guide to the Birds of Costa Rica. Cornell University Press, Ithaca, New York, USA.

Taylor, Ch. M. 1989. Revision of Palicourea (Rubiaceae) in Mexico and Central America. Systematic Botany Monographs 26.

Terborgh, J. 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. Ecology **52**:23-40.

Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. Ecology **58**:1007-1019.

Terborgh, J. 1985. The role of ecotones in the distribution of Andean birds. Ecology **66**:1237-1246.

Terborgh, J. and B. Winter. 1983. A method of setting parks and reserves with special reference to Colombia and Ecuador. Biological Conservation **27**:45-58.

Terborgh, J. and J. S. Weske. 1969. Colonization of secondary habitats by Peruvian birds. Ecology **50**:765-782.

Thiollay, J. M. 1992. Influence of selective logging on bird species diversity in a Guianan rain forest. Conservation Biology **6**:47-63.

Tilman, D. and J. A. Downing. 1994. Biodiversity and stability in grasslands. Nature **367**:363-365.

Tombesi, A., E. Antognozii and A. Pallioti. 1994. Optimum leaf area in T-bar trained kiwifruit vines. Journal of Horticultural Science **69**:339-350.

Turner, M. G., R. H. Gardner, and R. V. O'Neill. 1995. Ecological dynamics at broad scales. BioScience (Supplement):29-35.

Tutin, C. E. G. and M. Fernandez. 1993. Relationships between minimum temperature and fruit production in some tropical forest trees. Journal of Tropical Ecology **9**:241-248.

Uribe, D. A. 1986. Contribución al conocimiento de la avifauna del bosque muy húmedo montano bajo en las cercanías de Manizales. Tesis, Facultad de Medicina Veterinaria y Zootectnia, Universidad de Caldas, Manizales, Colombia.

van Wambeke, A. 1992. Soils of Tropics: Properties and Appraisal. McGraw-Hill, Inc., New York, NY.

Velásquez, A., H. Meyer, W. Marin, F. Ramírez, A. David, A. Campos, M. Hermelín, S. O. Bender, M. Arango and J. Serje. 1994. Planificación regional del occidente colombiano bajo consideración de las restricciones por amenazas. Memorias Conferencia Interamericana sobre Reducción de los Desastres Naturales, Cartagena de Indias, Colombia, Marzo 1994. Casa Impresora Pacífico, Santa Fé de Bogotá, Colombia.

Velásquez, M. P. 1992. Aves frugívoras y su relación con la flora en un bosque húmedo, en el municipio de San Carlos, Antioquia, Colombia. Trabajo de Investigación, Departamento de Biología, Universidad de Antioquia, Medellín, Colombia.

Velez, B. E. 1987. Contribución al estudio avifaunístico del Santuario de Fauna y Flora de Iguaque, Boyacá.Tesis, Departamento de Biología, Pontificia Universidad Javeriana, Santa Fé de Bogotá, Colombia.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos **57**:7-13.

von Ende, C. N. 1993. Repeated-measures analysis: Growth and other time-dependent measures. Pages 113-137, *in* S.M. Scheiner and J. Gurevitch, editors. Design and Analysis of Ecological Experiments, Chapman Hall, New York, NY.

Walker, L. R. and L. E. Neris. 1993. Posthurricane seed rain dynamics in Puerto Rico. Biotropica **25**:408-418.

Warburton, N. Structure and conservation of forest avifauna in isolated rainforest remnants in tropical Australia. *in* W. F. Laurance and R. O. Bierregaard, Jr., editors. Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities, *in press*.

Westoby, M., E. Jurado, and M. Leishman. 1992. Comparative evolutionary ecology of seed size. TREE **7**:368-372.

Wiens, J. A. 1992. Ecological flows across landscape boundaries: a conceptual overview. Pages 217-235, *in* A. J. Hansen and F. di Castri, editors. Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows. Springer-Verlag, New York, NW.

Wiens, J. A., C. S. Crawford and J. R. Gosz. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos **45**:421-427.

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237-256, *in* M.E. Soulé, editor. Conservation Biology: The

Science of Scarcity and Diversity. Sinauer, Sunderland, Massachusetts, USA.

Williams-Linera, G. 1990. Vegetation structure and environment of forest edges in Panama. Journal of Ecology **78**:356-373.

Winer, B. J., D. R. Brown and K. M. Michaels. 1991. Statistical Principles in Experimental Design. McGraw-Hill, New York, NY.

Wong, M. 1986. Trophic organization of understory birds in a Malasyan dipterocarp forest. Auk **103**:100-116.

Young, K. R. 1993. Woody and scandent plants on the edges of an Andean timberline. Bulletin of the Torrey Botanical Club **120**:1-18.

Zolman, J. F. 1993. Biostatistics: Experimental Design and Statistical Inference. Oxford University Press, New York, NY.

BIOGRAPHICAL SKETCH

I was born in the midst of a summer in Los Angeles, CA, to a Colombian couple. At that time my father was pursuing his Ph.D. degree in Mathematics and my mother was taking care of their two daughters. I got to spend a lot of time with my mother and she would tell me stories about her family, Colombia, and the activities of my father as a researcher. She also took the time to answer my questions, many of which had to do with the whys and hows of animal and plant life. Later on it was my mother's turn to complete her degree in the Social Sciences and for my father to take care of us. He would tell us stories of his own invention. It was from one of these that I learned that birds migrate and that not all individuals succeed. My compassion for other organisms was partially motivated by the little swallow that could never make it through its long journey.

By the time my parents moved back to Colombia, and after living in Mexico and Puerto Rico, I was conscious of my fascination for the living world. I knew that I wanted to unravel some of its misteries and one way to do so was to study Biology. At the Universidad del Valle I had plenty of opportunities to learn about biological principles, natural history, and politics. I found myself editing environmental newsletters, participating in human right groups, and discovering the pleasure of observing birds. For this I have to give credit to my former advisor, Humberto Alvarez-L. Birds and a two-month field season at the Sierra Nevada de Santa Marta were my gate into Ecology, which I have not abandoned since then.

The snowball has grown bigger, with lumps here and there, reminding me that my existence has not been plain. The time I spent at the University of Florida pursuing my Ph.D degree certainly shaped this snowball. The core remains pretty much unaltered, perhaps strengthened, and that is why some influential people in my life roll their eyes when I tell them my whereabouts. I do not know if this behavior is a warning signal "Carla you are getting into trouble" or a trusting signal "Carla you are going to make it". Perhaps it is a combination of both.

It seems that the snowball will continue to grow, as my eyes have widened so has the scale I want to look at things. I will spend the next two years doing post-doc work at Stanford University and at the University of Florida, adding further lumps to my life.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Douglas J. Levey, Chair
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

H. Jane Brockmann
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

C.S. Holling
Arthur R. Marshall, Jr., Professor of Ecological Sciences

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John Ewel
Professor of Botany

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Professor of Entomology and Nematology

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December, 1995

Dean, Graduate School